

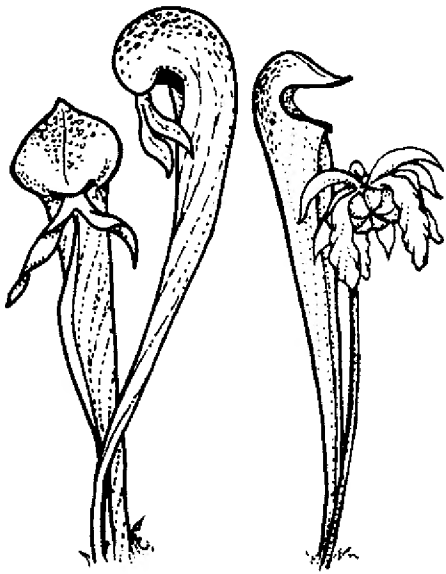
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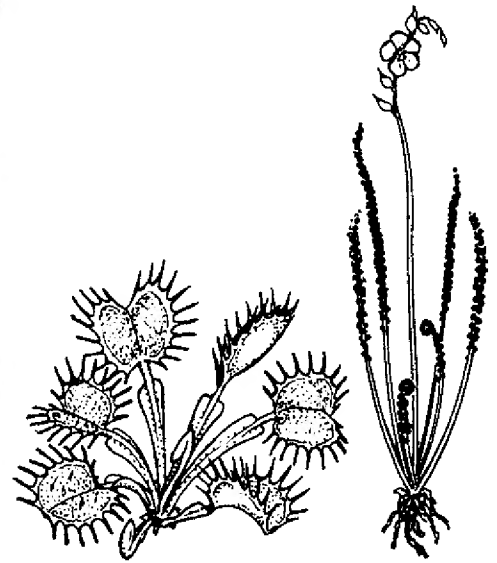




CARNIVOROUS PLANT NEWSLETTER

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Front Cover: *Drosera chrysolepis*, member of *Drosera* section *Brasiliae*, growing in the Serra do Cipó, Minas Gerais state, Brazil. Photo by Andreas Fleischmann. Article on page 4.

Back Cover: Paul Young standing next to his huge *Sarracenia* 'Leviathan'. Photo by Steve Sullivan. Article on page 36.

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A NEW SECTIONAL NAME FOR THE BRAZILIAN TETRAPLOID CLADE OF *DROSER*A SUBGENUS *DROSER*A

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Keywords: taxonomy, *Drosera* sect. *Brasiliae*, classification, phylogeny.

Historical infrageneric classifications of the genus *Drosera* L. (De Candolle 1824; Planchon 1848a, b; Diels 1906; Seine & Barthlott 1994; Schlauer 1996) took into account the external morphology of its species, especially style division, but also data from palynology (Takahashi & Sohma 1982), trichome morphology (Seine & Barthlott 1993; Länger *et al.* 1995) and chromosome numbers (e.g., Kondo 1976). Nevertheless, when confronted with the molecular phylogenetic reconstructions (Rivadavia *et al.* 2003, 2012), all existing classifications were unsuccessful in circumscribing a monophyletic *D.* section *Drosera*, due to the high homoplasy of morphological traits in that section. Hence, a new classification congruent with the phylogeny and based on monophyletic groups became necessary (Fleischmann *et al.* 2018).

The phylogenetic reconstructions of Rivadavia *et al.* (2003, 2012), based on the plastid marker *rbcL*, showed that all *Drosera* species, except for *D. regia* Stephens and *D. arcturi* Hook., belong to two large sister clades more or less geographically defined, an “Australian Clade” (*D.* subgen *Ergaleium*, comprising *D.* sections *Coelophylla*, *Lasiocephala*, *Bryastrum*, *Erythrorhiza*, *Stolonifera* and *Ergaleium*), and another clade representing an “out of Australia” movement. The latter has to be referred to as *D.* subgen. *Drosera* (as it contains the generic type, *D. rotundifolia* L.), with clades connected to basal nodes centered in Australia (*D.* sections *Arachnopus*, *Stelogyne*, *Prolifera*, *Psychophila*, *Thelocalyx*), and clades connected to more apical nodes of Neotropical and African distribution (*D.* sections *Ptycnostigma*, and *Drosera sensu* Seine & Barthlott 1994). In this topology, *D.* sect. *Drosera* (*sensu* Seine & Barthlott 1994) appears as paraphyletic with *D.* sect. *Ptycnostigma* nested within.

To better reflect the phylogenetic, geographical, and morphological groups, we adopted the topology of Rivadavia *et al.* (2012) for a new classification of the taxa hitherto placed in *D.* sect. *Drosera*. Therefore, *D.* sect. *Drosera* is here redefined as the clade containing *D. rotundifolia* (the type species of the genus), along with other temperate and diploid Neotropical taxa, as well as *D. spatulata* Labill and allied taxa. This clade is sister to two clades, the “African clade” (which contains *D.* sect. *Ptycnostigma*) and the “Brazilian Tetraploid clade” (Rivadavia *et al.* 2003, 2012; Gonella 2012). Consequently, *D.* sect. *Ptycnostigma* (whose type is *D. pauciflora* Banks ex DC.) is here expanded to include all taxa that fall within the “African clade”. Finally, the “Brazilian Tetraploid clade” remains unnamed, and a new sectional name is here proposed.

***Drosera* section *Brasiliae* Rivadavia, Gonella & A.Fleischm., sect. nov.**

Type: *Drosera graminifolia* A.St.-Hil., Hist. Pl. Remarq. Bresil 1(7): 269, t. 25C (1828).

This section comprises the species of the “Brazilian Tetraploid clade”, a monophyletic group that emerged in the phylogenetic reconstructions of Rivadavia *et al.* (2003, 2012). The sectional name

refers to the predominantly Brazilian distribution and the likely Brazilian origin of this evolutionary lineage.

Of the 18 species belonging to this section (Table 1), chromosome numbers are known for nine, which are consistently $2n = 40$ (Futagawa *et al.* 2002; Rivadavia *et al.* 2003; Rivadavia 2005). The species are also recognized by morphological characters such as an indumentum of translucent-yellow, short-stalked globose non-carnivorous trichomes in most species (Fig. 1; Gonella 2012; Gonella *et al.* 2014; Rivadavia *et al.* 2014; however, they are not an apomorphy for this section, these glands are also found in other species, e.g. *D. meristocaulis* Maguire & Wurdack, see Rivadavia *et al.* 2012), scapes often covered by a woolly indumentum of long, patent eglandular hairs and, most notably, circinate leaf veneration (Fig. 2; all except *D. tentaculata*, which is uniquely simple-geniculate among Brazilian sundews; Rivadavia *et al.* 2014). All sympatric members of other sections display geniculate-involute veneration (*D.* sects. *Bryastrum* and *Drosera*) or entire-involute veneration (*D.* sect. *Thelocalyx*) (Gonella 2012; Rivadavia *et al.* 2014).

Circinate leaf veneration is homoplastic in *Drosera*, as this characteristic appears independently in several lineages, including in three members of *D.* sect. *Drosera* (see below), and may be generally connected to more elongated leaf and lamina shapes (this is paralleled in the unrelated genus *Pinguicula* L. of Lamiales, where species with filiform leaves show circinate veneration). Such characteristic is also present in the three Andean species revised by Gonella *et al.* (2016), however, due to the unique combination of characters and the fact that these taxa were not sampled in any published molecular phylogenetic studies so far, these species remain unplaced for now.

Drosera* section *Drosera

Type: *Drosera rotundifolia* L.

=*Drosera* section *Rossolis* Planch., Ann. Sci. Nat., Bot., sér. 3(9): 92 (1824). *nom. superfl.*

=*Drosera* section *Eurossolis* Diels, Pflanzenr. 26: 62 (1906). *nom. superfl.*

=*Drosera* section *Oosperma* Schlauer, Carniv. Pl. Newslett. 25: 70 (1996).

Type: *Drosera intermedia* Hayne

Drosera sect. *Drosera*, as here redefined, includes all taxa belonging to the clade containing *D. rotundifolia* in the phylogeny of Rivadavia *et al.* (2012). Species of this section present chromo-

Table 1. Species included in <i>Drosera</i> sect. <i>Brasiliae</i> .	
#	Species
1	<i>D. ascendens</i> A.St.-Hil.
2	<i>D. camporupestris</i> Rivadavia
3	<i>D. chimaera</i> Gonella & Rivadavia
4	<i>D. chrysolepis</i> Taub. (Front Cover)
5	<i>D. graminifolia</i> A.St.-Hil.
6	<i>D. grantsauui</i> Rivadavia
7	<i>D. graomogolensis</i> T.R.S.Silva
8	<i>D. latifolia</i> (Eichl.) Gonella & Rivadavia
9	<i>D. magnifica</i> Rivadavia & Gonella
10	<i>D. montana</i> A.St.-Hil.
11	<i>D. quartzicola</i> Rivadavia & Gonella
12	<i>D. riparia</i> Rivadavia & Gonella
13	<i>D. schwackei</i> (Diels) Rivadavia
14	<i>D. spiralis</i> A.St.-Hil.
15	<i>D. spirocalyx</i> Rivadavia & Gonella
16	<i>D. tentaculata</i> Rivadavia
17	<i>D. tomentosa</i> A.St.-Hil.
18	<i>D. villosa</i> A.St.-Hil.

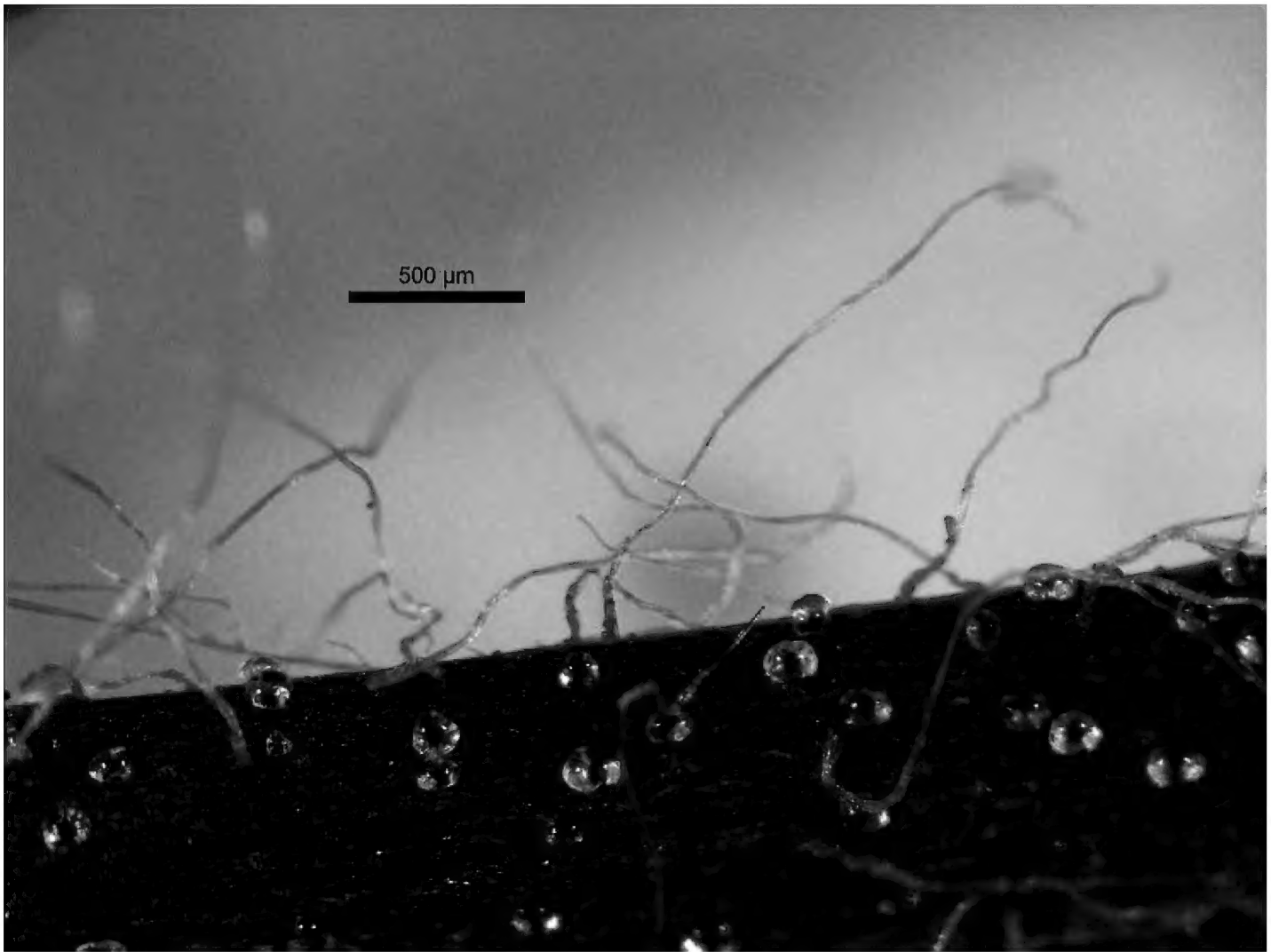


Figure 1: Indumentum of translucent-yellow, short-stalked globose non-carnivorous trichomes and eglandular hairs of the petiole of a herbarium specimen of *Drosera graminifolia*, the type species of *D.* sect. *Brasiliae*. Photo: Paulo M. Gonella.

some numbers of $2n = 20$ (except for *D. anglica* Huds., a species of amphiploid hybrid origin, with $2n = 40$; Rivadavia *et al.* 2003, and perhaps a few taxa of recent genome duplication). The species of the section are also characterized by spatulate leaves with geniculate-involute leaf vernation or, more rarely, circinate vernation in the species with linear leaves (*D. filiformis* Raf., *D. tracyi* (Diels) Macfarl. and *D. linearis* Goldie).

Drosera section *Oosperma* Schlauer (1996), was segregated from *D.* sect. *Drosera* based on the ovoid seed shape (vs. fusiform) and has as type-species *D. intermedia* Hayne. According to the topology found in the phylogenetic reconstruction of Rivadavia *et al.* (2012), ovoid seed shape is homoplastic, and taxa that would be classified as belonging to *D.* sect. *Oosperma* based on the section description provided by Schlauer (1996), can be found spread in *D.* sections *Drosera*, *Brasiliae* and *Ptycnostigma*. Hence, *Drosera* section *Oosperma* as circumscribed by Rivadavia (2003) is polyphyletic, as it additionally included four of the tetraploid Brazilian taxa, which belong to a different clade herewith classified as *D.* section *Brasiliae*. As the type of *D.* section *Oosperma*, *D. intermedia*, is part of the clade that is also comprising the generic type, *D. rotundifolia* (and hence the type of *D.* sect. *Drosera*), *D.* section *Oosperma* (*sensu* Schlauer 1996) is here placed under synonymy of *D.* sect. *Drosera*.

Drosera sect. *Brasiliae* is sister to a more widely circumscribed *D.* sect. *Ptycnostigma*, i.e. the clade comprising *D. pauciflora* and all other African sundews except *D. regia* and *D. indica* (Fleischmann *et al.* 2018):



Figure 2: Circinate leaf vernation of *Drosera villosa*: the leaf in bud of most members of *D. sect. Brasiliae* is enrolled like a mainspring or crozier – which distinguishes this affinity from other Neotropical *Drosera*. Photo: Paulo M. Gonella.

***Drosera* section *Ptycnostigma* Planchon**, Ann. Sci. Nat., Bot., sér. 3(9): 92-93 (1848).

Type: *Drosera pauciflora* Banks ex DC., Prodr. 1: 317 (1824).

=*Drosera* section *Crypterisma* Planchon, Ann. Sci. Nat., Bot., sér. 3(9): 92 (1824).

Type: *Drosera hilaris* Cham. & Schltdl.

=*Drosera* section *Vagae* Drude, Nat. Pflanzenfam. 3(2): 271 (1891).

Type: *Drosera capensis* L.

This section, as here redefined, includes all species belonging to the “African clade” in the phylogeny of Rivadavia *et al.* (2012), which comprises all *Drosera* species occurring on the African continent, with the exception of *D. regia* (*D. subgen. Regiae*) and *D. indica* L. (*D. sect. Arachnopus*). Regarding chromosome number, this section is quite heterogeneous, with variable numbers ($2n = 20, 40, 60$ or 80 ; Rivadavia *et al.* 2003). Most common leaf vernation pattern is geniculate-involute, but circinate is also present in some taxa (*D. pauciflora*, *D. alba* E.Phillips, and allied taxa).

In the original circumscription, Planchon (1848a, b) defined *D. sect. Ptycnostigma* as plants with flowers with multi-flabellate stigmata, succulent roots, and lacking stipules, containing only *D. cistiflora* L. and *D. pauciflora*. In the current expanded circumscription, all these three traits are not present in all taxa.

The summer-dormant, South African species with succulent roots (*D. cistiflora*, *D. pauciflora*, and allied taxa), which were segregated in *D. sect. Ptycnostigma* by Planchon (1848a, b; elevated to subgeneric rank by Diels 1906 and adopted by Schlauer 1996) are nested within a clade of African *Drosera* species (belonging to *D. section Drosera sensu* Diels 1906). The discrete classification of the summer-dormant species was reasoned by Planchon (1848a) based on the distinctive multifid-flabellate stigmata, a concept followed by Diels (1906), who even gave further weight to the stigma shape in his *D. subgenus Ptycnostigma*. However, this proved to be inconsistent, as the doubtlessly related *D. trinervia* (summer-dormant, stipules reduced) was not included in this affinity, but treated by Diels (1906) and subsequent authors in *D. subgen. Drosera*. Moreover, a grade of morphological characters connects the summer-dormant species of *D. subgen. Ptycnostigma* with the perennially growing species of *D. subgen. Drosera* (*sensu* Diels 1906). A clear example is the stipule reduction observed in *D. hilaris*, which connects to the stipule-lacking summer-dormant species circumscribed by Diels in his *D. subgen. Ptycnostigma*. *Drosera hilaris* was even placed in its own section, *Crypterisma*, by Planchon (1848a, b; spelled “*Cripterisma*” in the former source), based on its peculiar morphology. However, it is morphologically connected to the other South African *Drosera* species – both the perennially growing and the summer-dormant, hemicryptophyte species, to the former by overall flower morphology and to the latter by absence of stipules (Fleischmann *et al.* 2018). Further support is gained from molecular phylogenetic data, which show *D. hilaris* nested within a clade of South African *Drosera* species (Rivadavia *et al.* 2003), including those of *Ptycnostigma* (*sensu* Diels 1906).

Additionally, a similar type of non-carnivorous glandular trichomes was observed in all African *Drosera* species (except *D. regia* and *D. indica*) by Länger *et al.* (1995). Thus Seine & Barthlott (1994) correctly merged Planchon’s section/Diels’ subgenus *Ptycnostigma* with *D. subgenus Drosera*. However, as *D. section Drosera* proved to be paraphyletic (Rivadavia *et al.* 2003; Fleischmann *et al.* 2018), and as the clade comprising the African members does not contain the generic type, *D. rotundifolia*, Planchon’s sectional name *Ptycnostigma* is here re-elevated in a larger circumscription to classify all *Drosera* species of the African clade (*viz.* all species of *Drosera* that occur in Africa, excluding *D. indica* and *D. regia*).

The stigma shape of the summer-dormant species *D. cistiflora*, *D. pauciflora*, and allies is not a reliable taxonomic character for infrageneric classification, and rather seems to mirror adaptations to certain pollinator groups in these large-flowered species. The doubtlessly closely related *D. trinervia* (support comes from life strategy, morphology, and molecular data) does not share flabellate stigmata, but has simple spatulate-bifid stigmatic apices; in contrast, the only distantly related *D. regia* of *D. subgenus Regiae* also flabellate stigmata with multiple divisions.

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SUNDEW CHEMISTRY AND EMERGENCE UPDATES

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Keywords: *Drosera*, metabolism, phytochemistry, naphthoquinones, chemotaxonomy, micro-morphology, emergences.

Introduction

Plumbagin and 7-methyljuglone are characteristic acetogenic (= derived from acetic acid) naphthoquinones (see Scheme 1) that allow a chemotaxonomic delimitation and the distinction between sundew (*Drosera* L.) species or species groups (Zenk *et al.* 1969; Durand & Zenk 1974; Culham & Gornall 1994; Schlauer *et al.* 2005). This has recently (Schlauer *et al.* 2017) been applied to several Australian species in *Drosera* sections *Arachnopus* Planch. (the “*D. indica* L. complex”) and *Coelophylla* Planch. (*D. glanduligera* Lehm.). By extending these studies to further accessions and species, some new and interesting insights into the chemical diversity of the genus were gained. In addition, the characteristic leaf and stem emergences of all examined *Arachnopus* species are featured in detail by microscopy images.

Materials and Methods

All plants used in the present study were raised from seed. The geographic origin of all accessions was traced as far as possible (see Table 1). They were cultivated, harvested, and investigated under the same conditions applying the same methods as reported previously (Schlauer *et al.* 2017). Further accessions of several species already mentioned in that publication and of additional species were investigated in order to confirm their chemical characterization and/or to yield new results.

Mature (flowering) specimens of seven representatives of *D.* section *Arachnopus* were investigated for leaf and stem surface emergences by microscopy with a WILOSKOP F Zoom (Hund Wetzlar) with fiber light source FLQ 150 M (Hund Wetzlar) including swan neck fiber optics and a CMOS-camera UI1460LE-C (IDS Imaging Development Systems GmbH). The obtained images were enhanced for contrast and definition by MAGIX Foto & Grafik Designer (MAGIX Software GmbH) and EDIUS Workgroup 8.32 (Grass Valley K.K.).

Results

Naphthoquinones were detected in all investigated samples as summarized in Table 1.

Characteristic emergences for several species of *D.* section *Arachnopus* are shown in Figures 1–8.

Table 1. Species investigated in this study and quinones found.				
Section	Species	Accessions	Provenance	Quinone(s)
<i>Arachnopus</i>	<i>D. aurantiaca</i> *	1	Kimberleys, Australia	7-Methyljuglone
	<i>D. cucullata</i>	9	Kimberleys, Australia	Plumbagin
	<i>D. finlaysoniana</i>	4	Kimberleys, Australia	Plumbagin
		2	Queensland, Australia	Plumbagin
	<i>D. hartmeyerorum</i>	2	Kimberleys, Australia	7-Methyljuglone
	<i>D. indica</i>	1	Vietnam	7-Methyljuglone + Plumbagin
	<i>D. serpens</i>	3	Kimberleys, Australia	Plumbagin
		4	Queensland, Australia	Plumbagin
<i>Thelocalyx</i>	<i>D. burmannii</i>	1	Vietnam	7-Methyljuglone
	<i>D. sessilifolia</i> *	1	Brazil	7-Methyljuglone

*Species investigated here for the first time. NB: Earlier reports on *D. indica* quinones did not necessarily deal with this but possibly with different species of *D.* sect. *Arachnopus*.

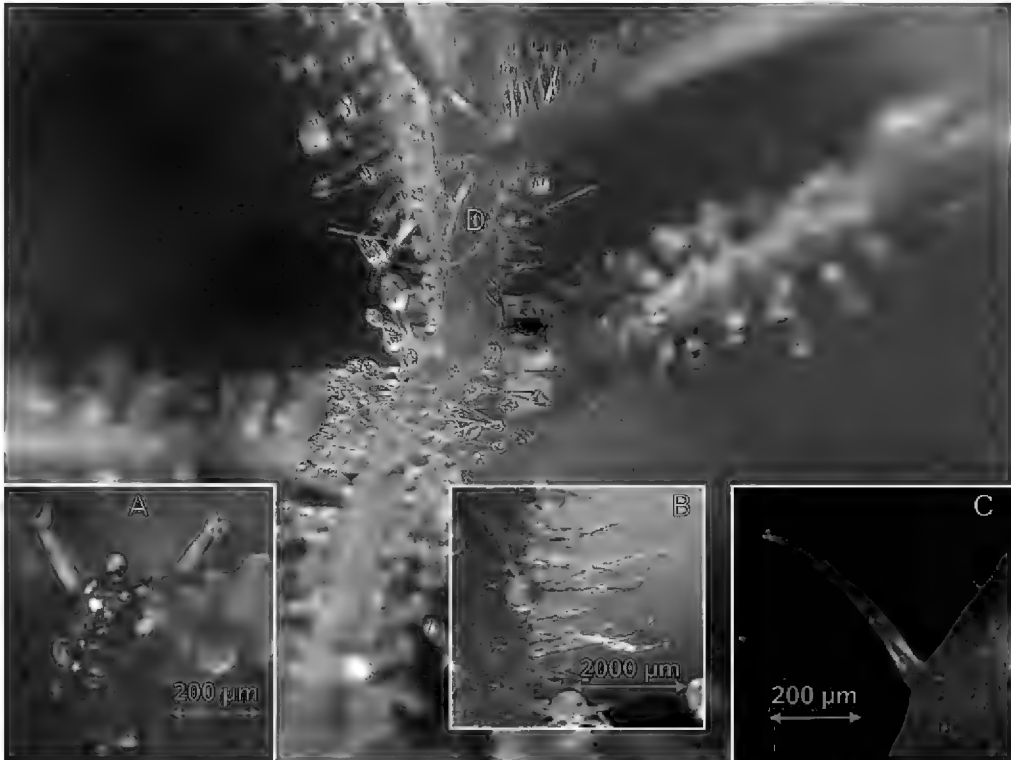


Figure 1: *Drosera aquatica*. Background: mature stem with leaf bases showing lateral “stipules” (actually emergences) at leaf bases (red arrows and oval); A: double-tipped cap emergences; B: elongated double-tipped caps (“hairs”) and stalked glands on stem; C: elongated double-tipped cap at side of leaf base.

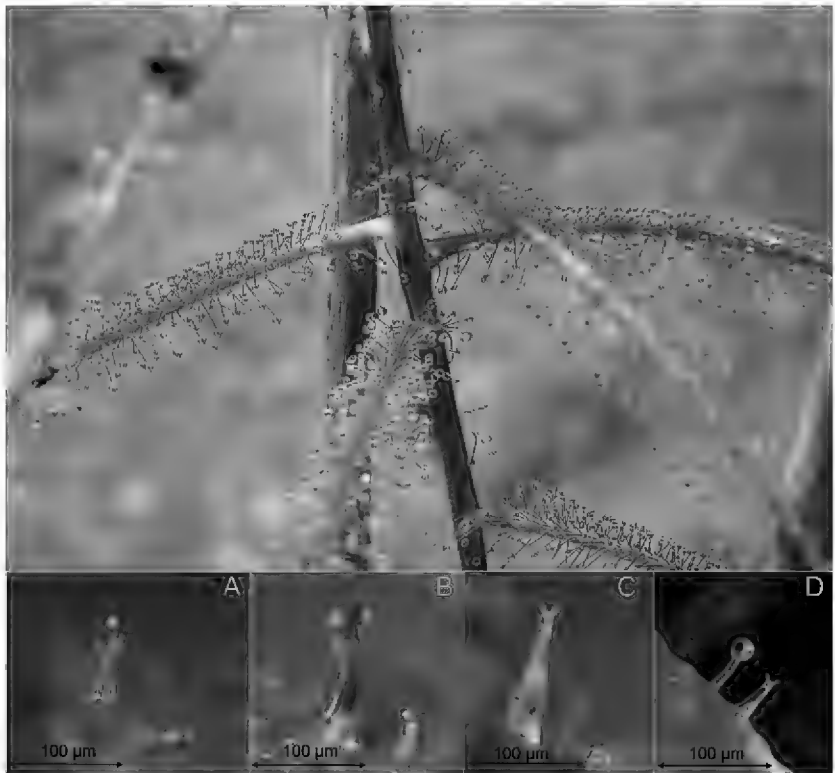


Figure 2: *Drosera aurantiaca*. Background: mature stem with leaf bases; A: mushroom-shaped emergences; B: a small double-tipped cap emergence (right) and a longer mushroom-shaped stalked gland (left) with beginning excrescence (transition to bulls-head shape?) on either side; C: long double-tipped cap (left) and stunted form (right); D: short stalked gland (left) and double-tipped cap (right).

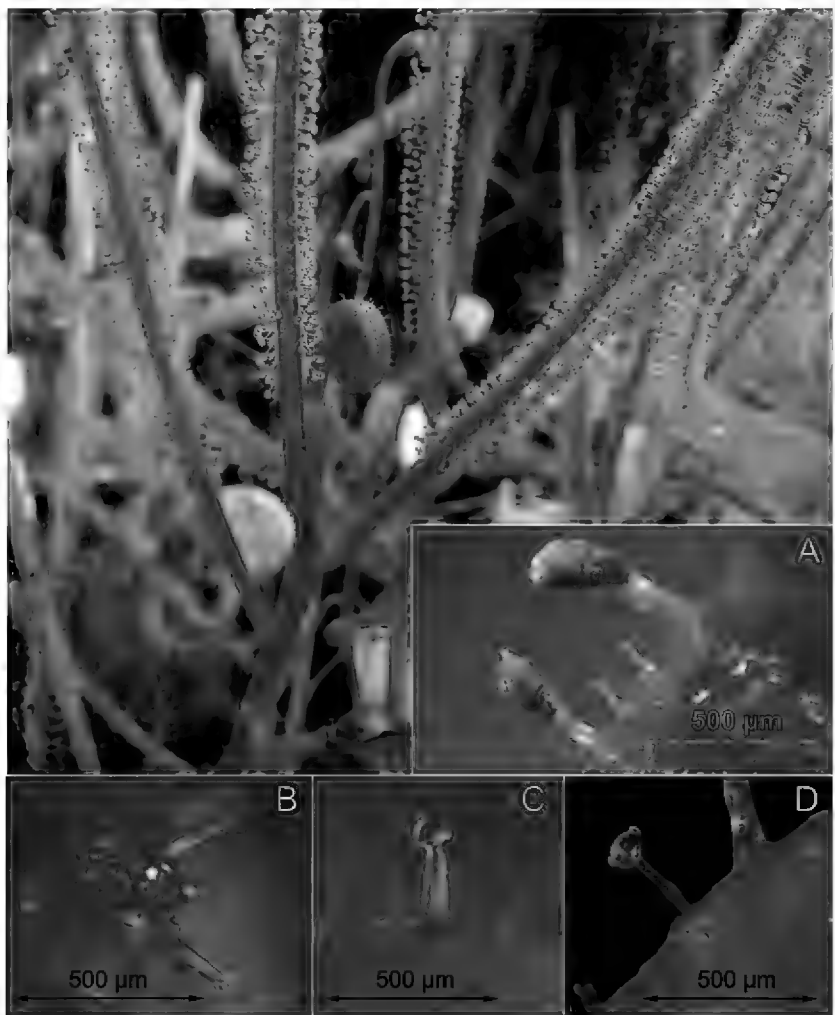


Figure 3: *Drosera cucullata*. Background: mature stem with leaf bases; A: insect- abdomen-shaped emergences (large) and small double tipped caps with almost completely round head (center); B: double-tipped caps; C: mushroom-shaped emergence; D: mushroom-bulls-head transition and small double tipped cap (left).



Figure 4: *Drosera finlaysoniana*. Background: mature stem with leaf bases; A: double-tipped caps; B: mushroom-shaped emergence; C: bulls-head with translucent center.

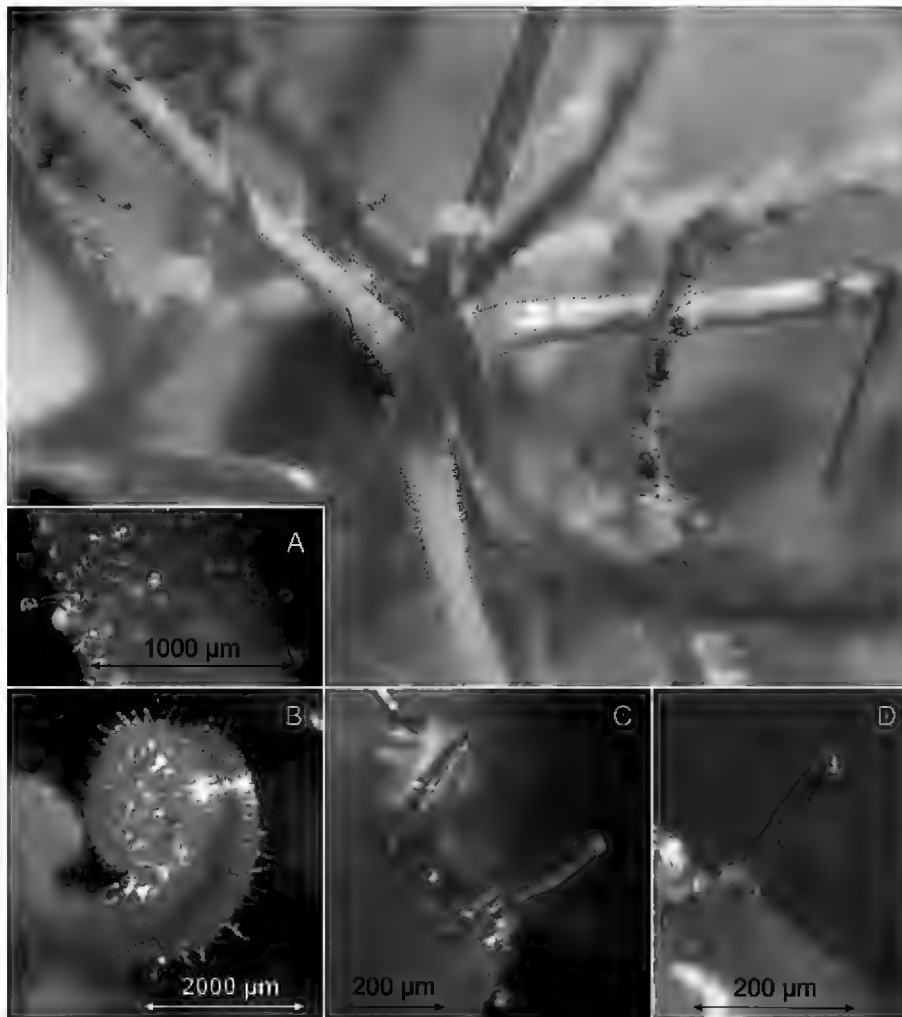


Figure 5: *Drosera fragrans*. Background: mature stem with leaf bases; A: stalked glands; B: involute leaf bud viewed from abaxial side showing double-tipped caps; C: double-tipped caps; D: double-tipped cap with almost completely round head.

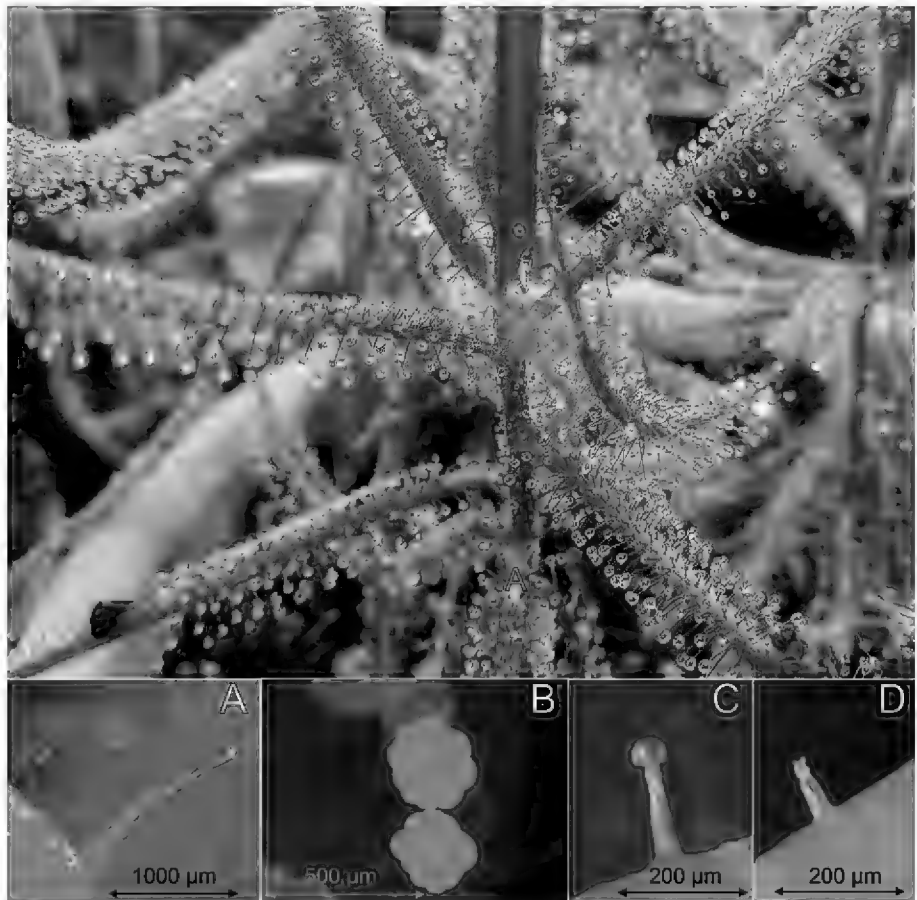


Figure 6: *Drosera hartmeyerorum*. Background: mature stem with leaf bases; A: double-tipped cap with elongated stalk at leaf bases (red arrows); B: moriform emergence showing giant cells; C: mushroom-emergence; D: double-tipped cap.



Figure 7: *Drosera indica*. Background: mature stem with leaf bases showing lateral "stipules" (actually emergences) at leaf bases (red arrows and oval); A: double-tipped cap with elongated stalk at leaf base with stalked glands and short double-tipped caps; B: mushroom-emergence (left), shorter stalked glands and medium sized double-tipped cap.



Figure 8: *Drosera serpens*. Background: mature stem with leaf bases; A: double-tipped caps (short) and insect-abdomen-emergences (long); B: bowler-hat-emergence (right) and double-tipped cap (left); C: bulls-head emergence with yellow center.

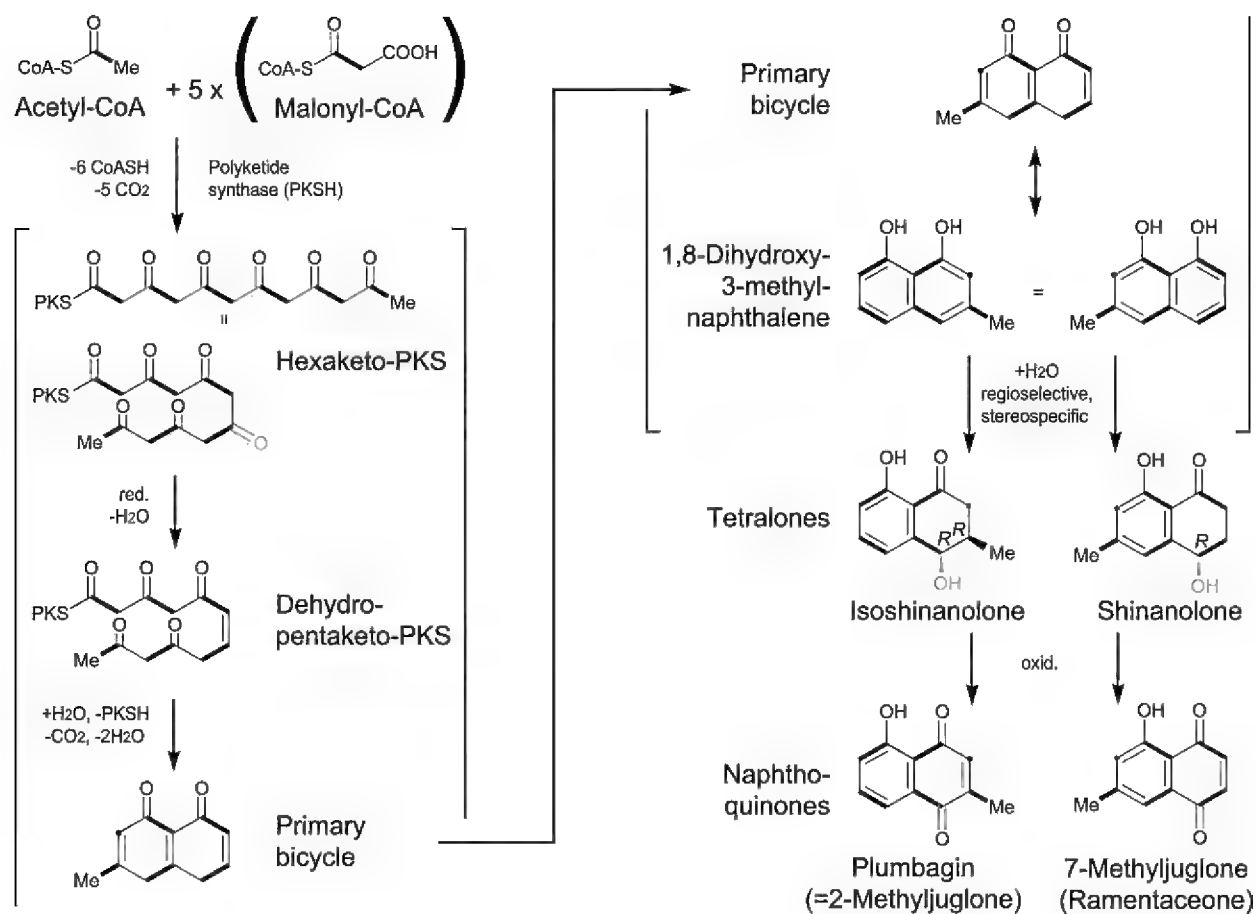
Discussion

The naphthoquinones detected in the investigated species of *D.* section *Arachnopus* confirm the chemical diversity as outlined previously (Schlauer *et al.* 2017). The constant chemism of the frequent species *D. serpens* Planch. and *D. finlaysoniana* Wall. ex Planch. across all investigated accessions demonstrates the reliability of quinones as chemotaxonomic markers.

Among species that lack distinct petioles (like e.g., *D. aurantiaca* Lowrie, *D. aquatica* Lowrie, or *D. hartmeyerorum* Schlauer), *D. finlaysoniana* is noteworthy as the only one known to contain plumbagin instead of 7-methyljuglone.

Most unusual is the detection of both plumbagin and 7-methyljuglone in *D. indica* s. str. So far both have only been found together in the same plant in hybridogenic taxa (Schlauer & Fleischmann 2016). Within its whole range (from western tropical Africa to East Asia, including China and Japan) *D. indica* is so far known to come into contact with only two species of *D.* section *Arachnopus* (*D. finlaysoniana* and *D. serpens*), both known to contain plumbagin and not 7-methyljuglone, so no potential parent contributing the ability to form 7-methyljuglone can be postulated. Perhaps the formation of both quinones in *D. indica* is a rare case of loss of regioselectivity in the biosynthesis of these metabolites (possibly at the stage of formation of the tetralones, see Scheme 1).

The detection of 7-methyljuglone in both species of *D.* section *Thelocalyx* Planch. confirms previous reports for *D. burmannii* Vahl (Culham & Gornall 1994) and underlines a close relationship between both species that is also expressed in a high degree of morphological overlap between them.



Scheme 1: Hypothetical biosynthesis of naphthoquinones in *Drosera*. Acetate-derived C₂ units shown as bold lines, resulting C₁ units as filled circles.

Our results stand in sharp contrast to the purported presence of plumbagin in *D. burmannii* (Putalun *et al.* 2010), and we attribute this doubtful record to an inappropriate detection method (immunoassay without exclusion of cross-reactivity against 7-methyljuglone) in the latter study.

In contrast to (intrapetiolar) stipules that are leaf like outgrowths along the whole length of the dividing line between the upper (adaxial) surface of the leaves and the stem in *Drosera*, emergences have their base limited to a small area only a few cells in diameter on the surface of leaves or stems. By this definition and based on the fact that they are frequently terminated by two tips (like in the common double-tipped cap emergences), the structures previously described as stipules in *D. sect. Arachnopus* are identified as emergences here.

Acknowledgements: This work significantly benefitted from the generous donation of seeds by Gideon Lim, Selangor, Malaysia, for which we have the pleasure to express our gratitude.

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WHAT'S NEW IN THE WORLD OF CARNIVOROUS PLANTS — SUMMARY OF TWO SYMPOSIA HELD IN JULY 2017

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Dozens of scientific papers about carnivorous plant research are published each year on diverse topics ranging from new species descriptions, through phylogenetic approaches in taxonomy and systematics, to ecology and evolution of botanical carnivory, biomechanics and physiology of traps, among many others. By the time a paper is published, however, it is already “old news” because the salient results often are presented months or even years earlier at scientific conferences. Such meetings are the perfect venues to discuss ongoing research and “hot” topics and present them to colleagues from around the world.

The first and last authors of this report were in the lucky situation to organize symposia about carnivorous plant biology during two major conferences: Simon Poppinga chaired a one-day session—“Carnivorous plants - Physiology, ecology, and evolution”—on July 6, 2017, as part of the Annual Main Meeting of the Society for Experimental Biology (SEB) in Gothenburg, Sweden. This first symposium included two keynote and two invited talks given by renowned carnivorous plants experts and six additional lectures. Aaron Ellison chaired a half-day session co-organized with Bartosz Płachno—“Evolution, ecology, and physiology of carnivorous plants”—on July 25, 2017, as part of the XIX International Botanical Congress (IBC) in Shenzhen, China. This second symposium included 11 invited talks.

These two symposia harkened back to the 1980 SEB symposium on carnivorous plants organized by Barrie Juniper (Fig. 1; see also the review by Williams (1981)) that led to the well-known book *The Carnivorous Plants* (written by Juniper, Richard Robins, and Danny Joel, published in 1989), and presaged the new publication (December 2017) of *Carnivorous Plants: Physiology, Ecology, and Evolution* (edited by Aaron Ellison and Lubomír Adamec). This summary aims to inform the CPN readership about the research presented at these two symposia.

Present at both symposia, Dr. Andreas Fleischmann discussed the multiple evolutionary lines of carnivorous plants. Current research shows that carnivory has evolved at least ten times in flowering plants, resulting in 19 carnivorous plant genera containing at least 800 species (Fig. 2). Five basic trap

SOCIETY *for* EXPERIMENTAL BIOLOGY

OXFORD CONFERENCE — DECEMBER 1980

CARNIVOROUS PLANTS I

(Botany Lecture Theatre)

Organised by: B. E. JUNIPER

Chairman: B. E. JUNIPER

- 9.00 J. HESLOP-HARRISON (Aberystwyth): The physiology of secretion and absorption by leaf glands of *Pinguicula*.

Enzyme secretion is driven by the passage of water through the gland accompanying the movement of Cl⁻ ions from a basal reservoir cell, apoplastic flow being blocked by an intervening endodermal cell. During resorption, control is lost, and the digest pool enters the leaf through endodermal and reservoir cells.

- 9.40 R. J. ROBINS and B. E. JUNIPER (East Anglia and Oxford): The secretory cycle of *Dionaea muscipula*.

Stimulation of the digestive organs evokes the release of hydrolytic activity from stores within the smooth endoplasmic reticulum, a subcompartment of the vacuole and the cell wall. Release primarily appears to occur by fusion of the smooth endoplasmic reticulum to the plasmalemma. Additional *de novo* synthesis provides further protein for secretion and replenishes the stores.

- 10.20 P. REA (Oxford): Fluid secretion and absorptive activity in the glands of *Dionaea muscipula*.

Stimulation of the digestive glands of *Dionaea* elicits a secretion of chloride ions together with protons. Evidence is presented concerning the mechanism of chloride transport and the relevance of proton extrusion to amino acid uptake.

- 10.40 COFFEE.

- 11.00 Y. HESLOP-HARRISON (Aberystwyth): The comparative morphology of the enzyme secretory glands of *Genlisea*, *Pinguicula* and *Utricularia* (Lentibulariaceae) and *Byblis* (Byblidaceae).

The digestive glands of carnivorous plants have a basic architecture of three cell types: (a) secretory, (b) endodermal and (c) reservoir or communicatory. There are, however, some departures in detail in gland morphology, both fine structural and cytochemical, and probably also in function. These features will be compared in four genera.

- 11.40 U. LÜTTGE (Darmstadt): Transport by the glands of carnivorous plants in relation to other glands and comparable systems.

- 12.20 S. E. WILLIAMS (Lebanon Valley College, U.S.A.): The comparative physiology of the prey capture mechanism of the Droseraceae.

The capture movements of *Dionaea* and *Drosera* are controlled by mechanically initiated action potentials and a chemically initiated hormonal mechanism. The rapid movements of *Drosera* result from changes in wall plasticity while those of *Dionaea* appear to involve a combination of a turgor change mechanism with a plasticity change mechanism.

- 1.00 LUNCH.

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CARNIVOROUS PLANTS II

Chairman: R. J. ROBINS

- 2.15 THE BOTANIC GARDEN, HIGH STREET.

J. K. BURRAS (Oxford): The culture and propagation of carnivorous plants.

- 4.00 TEA (in the Botany School, South Parks Road).

- 4.30 D. JOEL and B. E. JUNIPER (Jerusalem and Oxford): The structure of the

glands of *Drosophyllum lusitanicum* and *Dionaea muscipula* in relation to absorption. The dye neutral red cannot be absorbed by the glands of *Drosophyllum* when young nor by those of *Dionaea* before stimulation. Both sets of glands have very thin cuticles; that of *Drosophyllum* becomes permeable at maturity and that of *Dionaea* after stimulation. The ultrastructural changes will be described and a hypothesis for this absorption control proposed.

- 5.30—6.10 THE TENDER TRAP. A film of carnivorous plants by Oxford Scientific Films.

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Figure 1: Schedule of the 1980 symposium on carnivorous plants presented at the Oxford Conference of the Society of Experimental Biology, December 1980. Thanks go to Prof. Stephen Williams for providing the scans.

Carnivorous plants

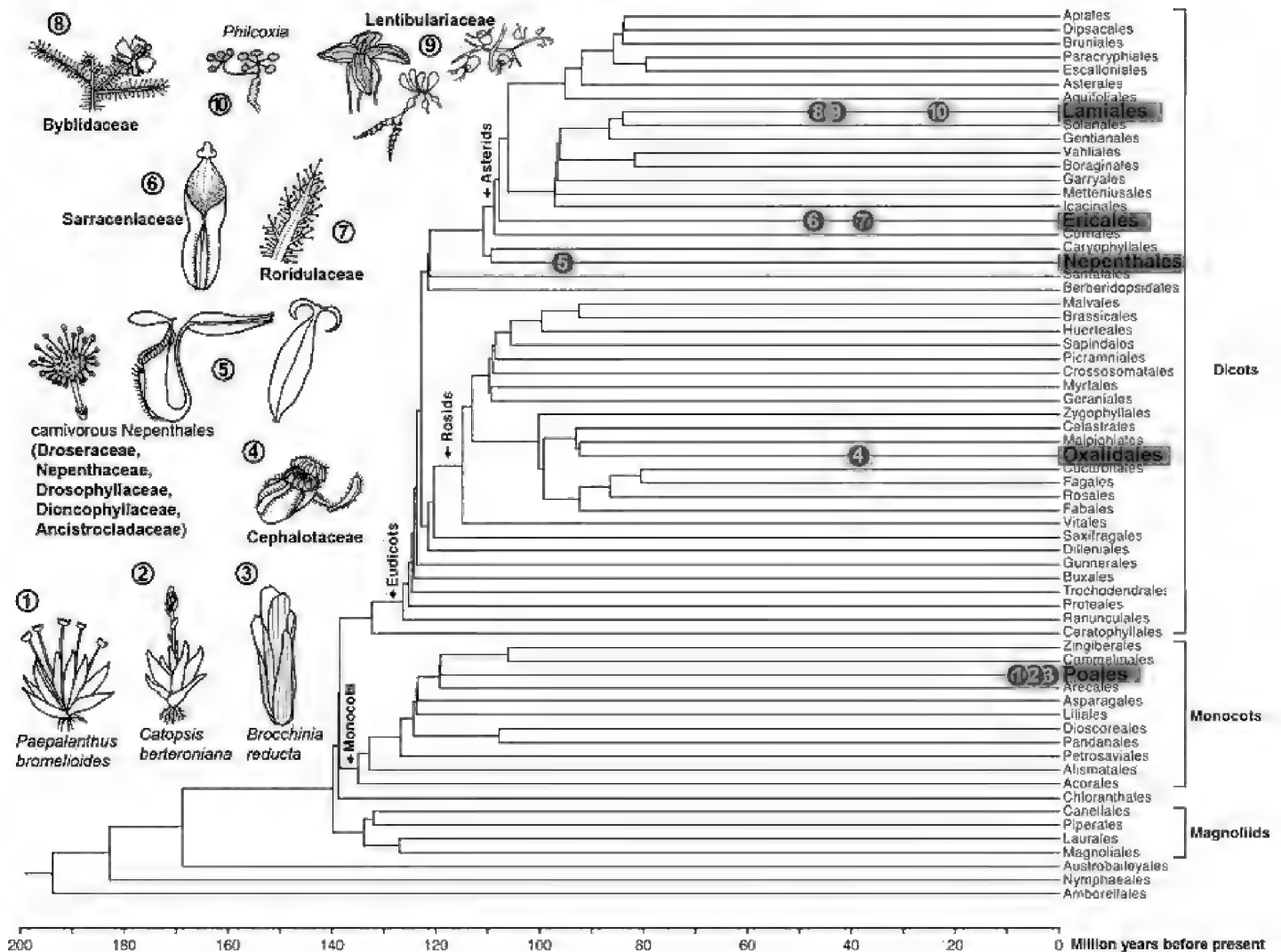


Figure 2: Family tree of the flowering plants, with botanical orders containing carnivorous plants highlighted in green. Evolutionary origins of carnivorous lineages indicated by red dots. The further to the left the dot on a branch, the older the carnivorous lineage. Figure modified from Fleischmann *et al.* 2017, and reprinted with permission of Oxford University Press.

types are found among carnivorous plants (pitfall traps, adhesive traps, snap traps, eel traps, and suction traps; Fig. 3). Some trap types (especially motile traps such as suction traps or snap traps) have evolved as modifications of passive flypaper-type traps within the same lineage (“homology”), but others have evolved in parallel in distantly related groups (“homoplasy” or convergent evolution). Prof. Aaron Ellison also gave talks in both symposia, where he presented a comprehensive synopsis on how carnivorous plants can be used as experimental systems to address contemporary scientific problems. His review included discussions of how carnivorous plants have illuminated studies of evolutionary convergence, inspired biomimetic materials, been used to study complex ecological questions about food-web assembly, and led to the development of school curricula and citizen science programs.

Studies of the morphology and the genomes of carnivorous plants continue to yield new and often surprising results. At the IBC symposium, Mathias Scharmann showed that population genomics of naturally co-occurring *Nepenthes* species in Southeast Asia are clearly distinct but not yet reproductively isolated (Fig. 4). The maintenance of genetic and phenotypic identities in the presence of gene flow indicates adaptive processes, presumably through selection against certain hybrids. Mr. Firman Alamsyah used both molecular data (internal transcribed spacer sequences of nuclear DNA) and morphological data on peristome structure to illuminate evolutionary trends in

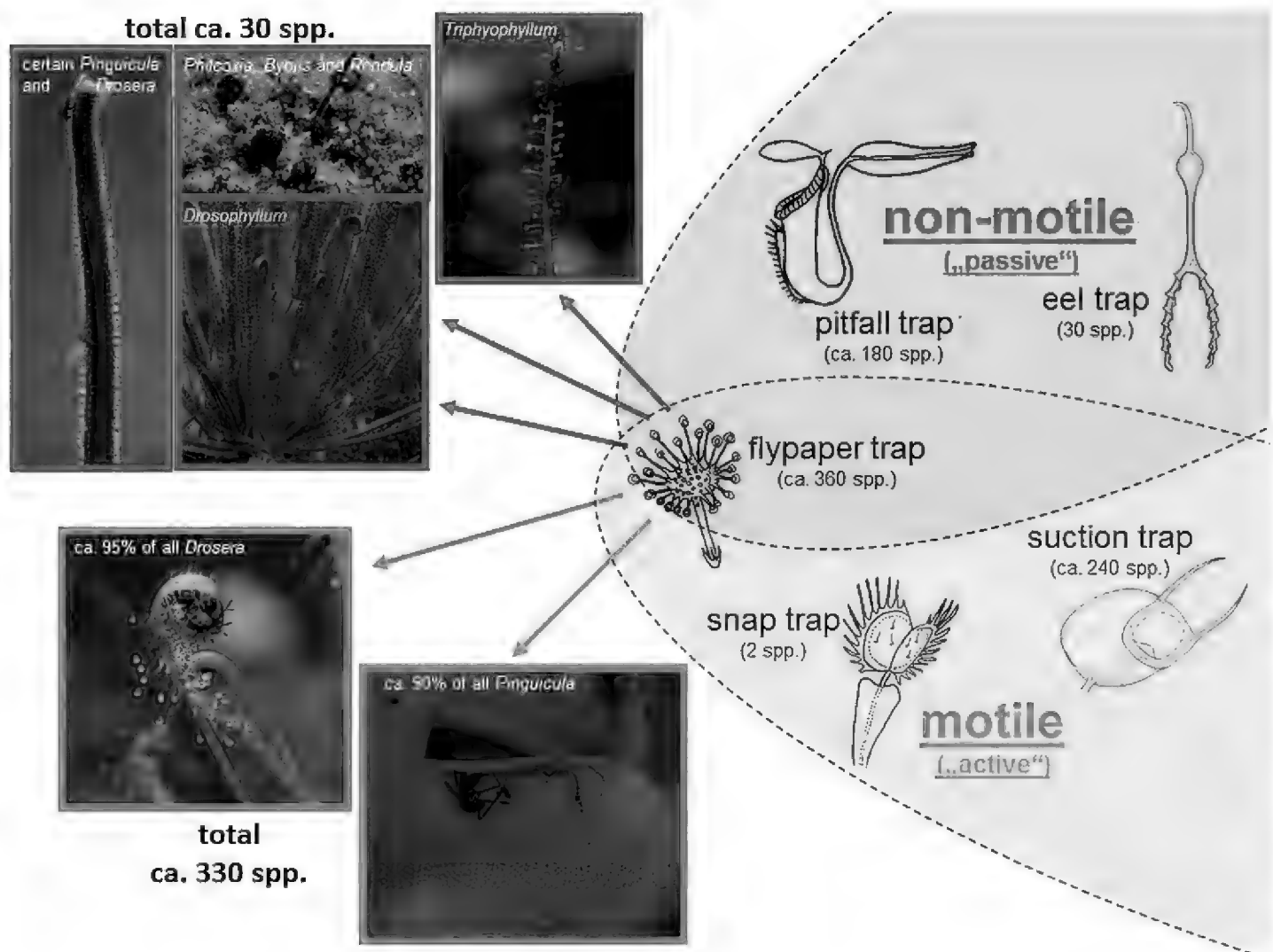


Figure 3: Distribution of the 5 basic trap types among the ≈ 800 species of currently known carnivorous plants. The trap types can be classified as motile or non-motile, depending upon capability of motion for prey capture or retention. Among the plants with sticky traps, there are those motile and non-motile passive leaves. Photographs and drawings by Andreas Fleischmann.

Nepenthes. He reported that narrow (< 10 -mm) peristomes appear to be the ancestral (“plesiomorphic”) condition in the genus, and that larger (10–20-mm or > 20 -mm) peristomes likely evolved at least 7 and 8 times, respectively, whereas the narrow peristome evolved again at least 4 times from lineages with wider peristomes (Fig. 5). In a second talk, Alamsyah reported new results on molecular evolution of the nepenthesin II digestive enzyme in 29 species of *Nepenthes*. These results soon will be submitted for peer review and eventual publication.

Dr. Bartosz Płachno and colleagues (Małgorzata Stpiczyńska, Richard W. Jobson, Hans Lambers) presented new research on glands and other features of the flowers of carnivorous plants. Although most carnivorous plant enthusiasts focus on the traps, the flowers not only are beautiful (Fig. 6) but also need specific adaptations so pollinators don’t end up as prey (Cross *et al.* 2017). Like the unique glandular hairs of carnivorous traps, the entomophilous species of *Pinguicula*, *Genlisea*, and *Utricularia* also have specialized glandular hairs on their flowers. These produce fragrances or nectar to attract pollinators.

Prey capture and its importance for carnivorous plant growth continues to inspire both basic and applied research. In the SEB symposium, Prof. Ulrike Müller explained the fluid mechanics during prey capture by the suction traps of bladderworts (*Utricularia vulgaris* and *U. gibba*) and presented fascinating and new insights into these enigmatic and extremely complex mechanical trap devices. Dr. Sebastian Kruppert and Martin Horstmann reported research on carnivorous plants from the

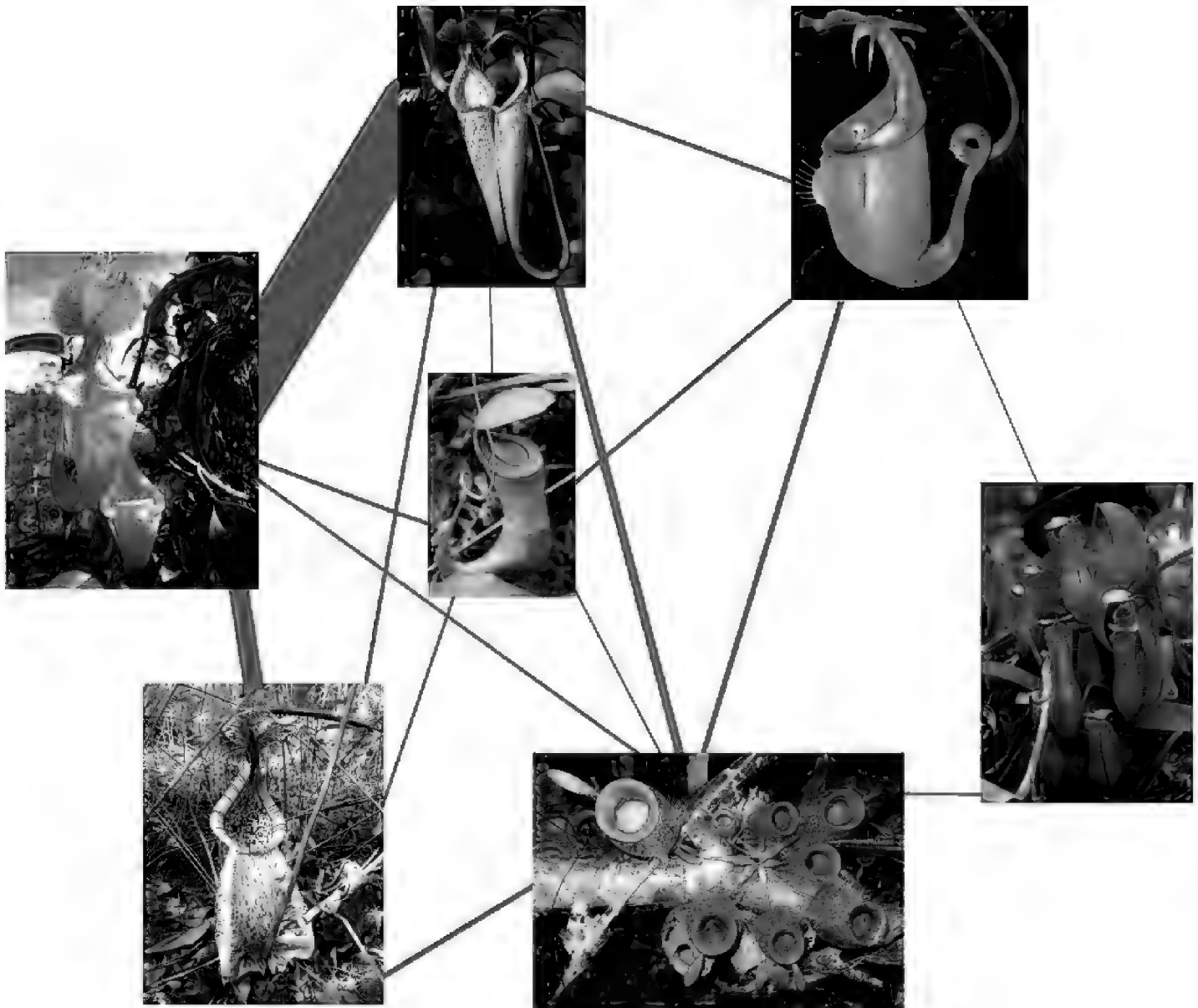


Figure 4: Network of gene flow between seven *Nepenthes* spp. that grow together in the same or adjacent habitats in the lowlands of Borneo (clockwise from above): *Nepenthes hemsleyana*, upper pitchers; *N. bicalcarata*, upper pitcher; *N. gracilis*, lower pitchers; *N. ampullaria*, rosette with lower pitchers; *N. rafflesiana* giant form, lower pitcher; *N. rafflesiana* typical form, upper pitchers; center: *N. mirabilis*, upper pitcher. Population genomics have revealed that hybridization and back-crossing has been occurring between some of these species for thousands of generations. Gene flow and its estimated strength is shown by the thickness of the green bars. All photographs by Mathias Scharmann.

perspective of the prey. They showed how freshwater crustaceans react to botanical predators with inducible morphological changes that impede capture. Three weeks later at the IBC symposium, Ms. Saskia Klink (with her colleagues Philipp Gieseemann and Gerhard Gebauer) presented new estimates of the amount of nitrogen obtained from prey by *Pinguicula* and *Utricularia* growing in Austria and Germany. By measuring the concentration of stable isotopes of nitrogen, Klink *et al.* showed that prey contribute about as much nitrogen to *Pinguicula* and *Utricularia* as they do for other sticky leaf (*Drosera* spp.) and aquatic (*Utricularia* subgenus *Polypompholyx*) carnivorous plants. They conclude that a closer look at the trophic levels of prey organisms can improve our understanding of the performance of carnivorous plants in their specific habitats.

In the IBC symposium, the themes of evolutionary convergence and prey capture came together in Ms. Laura Skates’s talk. She presented part of her ongoing PhD research (done in collaboration with Maria Paniw, Fernando Ojeda, Kingsley Dixon, Gerhard Gebauer, Jason Stevens, and Adam

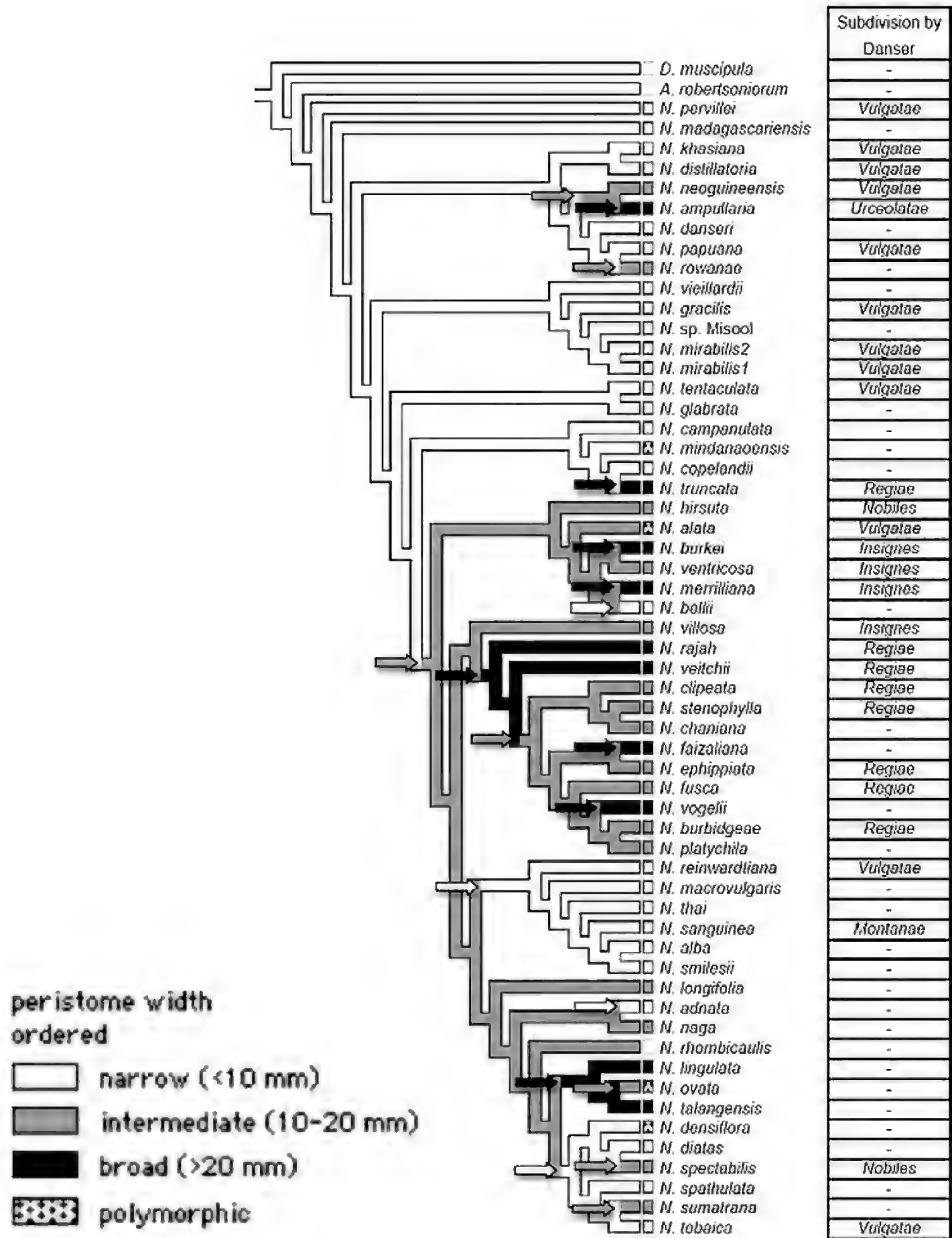


Figure 5: Character state reconstruction of *Nepenthes* for peristomes. Arrows indicate repeated evolution of narrow, intermediate, and broad peristomes (figure modified from Alamsyah & Ito 2013).

Cross) on the convergent evolution of the rainbow plant, *Byblis gigantea*, and the dewy pine, *Droserophyllum lusitanicum*, with respect to the relationship between their investment in carnivorous structures and the reliance on carnivory of these two species (Fig. 7). She discussed the ecological relevance of prey capture for each species and the implications for their management and conserva-



Figure 6: Flowers of *Utricularia bremii* photographed by Bartosz Płachno in sand-pit Cep I in Suchdol nad Lužnicí, S. Bohemia (Czech Republic).

tion. Tom Givnish presented an updated version of his influential cost/benefit model for the evolution of carnivory in plants.

In the SEB symposium, Dr. Ulrike Bauer reviewed the biomechanics of pitfall traps, explained how arthropods lose their foothold on them, and how such slippery pitcher-plant surfaces are inspiring novel technologies. Anna Westermeier gave new and fascinating insights into the trapping mechanics of the Venus’ flytrap’s little aquatic sister, the waterwheel plant (*Aldrovanda vesiculosa*), based on comprehensive biomechanical experiments and theoretical modelling. Dr. Simon Poppinga presented an overview of recent research about the snapping behavior of the Venus’ flytrap. Westermeier’s and Poppinga’s projects both are within the Collaborative Research Centre 141 and are part of a broader effort at the University of Freiburg in which the movements of carnivorous plants are being studied for development of biomimetic applications (Poppinga *et al.* 2016).

Two presentations, one at SEB and the other at IBC, examined commensal organisms, also known as inquilines, that inhabit the traps of different carnivorous plants. At the SEB, Dr. Dagmara Sirová discussed the highly complex plant-microbe interactions in the carnivorous bladderworts (*Utricularia*). Many researchers have observed living and reproducing algae and eukaryotes inside the bladders, and Sirová and her colleagues are developing the *Utricularia* system as a model for studying host-microbe interactions and their ecological dynamics (Sirová *et al.* 2017). At the IBC, Ms. Amanda Northrop presented work that she and her colleagues (Rachel Brooks, Jéssica Duarte Sousa, Aaron Ellison, Bryan Ballif, and Nicholas Gotelli) are doing to develop the purple pitcher plant, *Sarracenia purpurea* and its bacterial inquilines as a model system for understanding and predicting the dynamics of aquatic ecosystems and tipping points between aerobic and anaerobic



Figure 7: Leaves of *Byblis gigantea* (left) and *Drosophyllum lusitanicum* (right). Photographs by Laura Skates.

states. Northrop *et al.* use metagenomics and metaproteomics to identify differences in the composition and function of bacteria in pitchers with or without excess prey (Fig. 8). They showed that the *S. purpurea* micro-ecosystem can be experimentally manipulated to undergo a state change, that such states can be distinguished using environmental proteomics methods, and that these findings from the *S. purpurea* model micro-ecosystem may be applicable to larger aquatic ecosystems.

Finally, one speaker at each symposium discussed possible new additions to the carnivorous flora. At the SEB, Dr. Anneke Prins presented her ongoing investigations into the proto-carnivorous properties of common teasel (*Dipsacus fullonum* [Caprifoliaceae: Dipsacales]). At the IBC, Mr. Qianshi Lin discussed his dissertation work (co-authored with T. Gregory Ross, Fushi Ke, and Sean Graham) on the possibilities of carnivory in Canadian species of *Triantha* (Tofieldiaceae: Alismatales) that grow in bogs side-by-side with *Drosera* and *Pinguicula*. In both cases, further experimental work is ongoing to determine whether these plants possess all the characteristics of the “carnivorous syndrome” (Ellison & Adamec 2017).

With many people in the audience actively working on carnivorous plants, each talk was accompanied by thorough discussion. The inspiring and exciting atmosphere also was supported by the great venues. The many original research presentations about carnivorous plant-prey interactions, sophisticated fluid mechanics, evaluation of the “carnivorous status” of a certain species, and trapping mechanics will, once published, surely have a great impact in a variety of research fields. Many of the speakers who presented at the symposia can be seen in the group photos (Fig. 9). Because the SEB symposium was on the same day as the birthday of our highly esteemed colleague and friend,

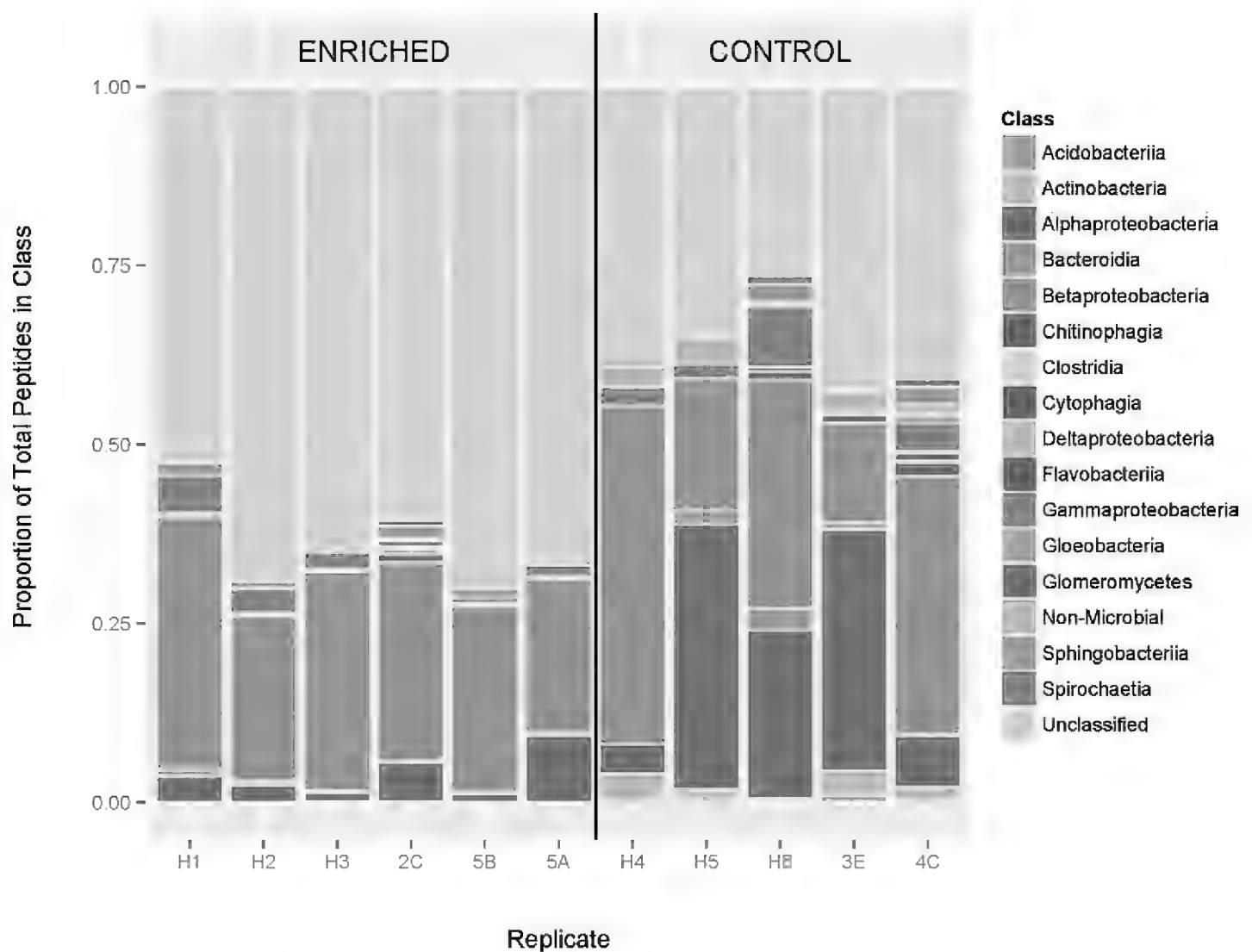


Figure 8: Distinctly different microbial communities contribute to protein expression in unfed and fed *Sarracenia purpurea* pitchers. The bars illustrate the proportion of total peptides from the top 220 proteins associated with specific microbial classes. Figure from Northrop *et al.* (2017) and reproduced with permission of the Ecological Society of America.



Figure 9: Left: SEB group photo with birthday greetings to Dr. Lubomir Adamec, and participants (left to right): Sebastian Kruppert, Ulrike Müller, Martin Horstmann, Anneke Prins, Dagmara Sirová, Aaron Ellison, Anna Westermeier, Simon Poppinga, Andreas Fleischmann. Presenter Ulrike Bauer is not in the photograph. Right: ICB group photo, with participants (left to right): Mathias Scharmann, Firman Alamsyah, Aaron Ellison, Saskia Klink, Bartosz Płachno, Amanda Northrop, Qianshi Lin, Laura Skates, Adam Cross. Presenter Tom Givnish is not in the photograph.

Dr. Lubomir Adamec (Trebou, Czech Republic), we added a special greeting to him, which we sent to him from the conference (Fig. 9).

Acknowledgments: SP & AW's projects are supported within the Collaborate Research Centre 141. UB is funded by a Royal Society University Research Fellowship. FA's participation at the XIX IBC was supported by a Scholar award from the IBC Committee and funds from Prof. Dedy Darnaedi (Researchers Care Group). UKM is supported by grant 13-52130 from the US National Science Foundation (NSF). AN was funded by NSF grants 11-44055 and 11-44056 and an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health under grant number P20GM103449. The Botanical Society of America provided partial support for AN to attend the XIX IBC. LS is supported by a Research Training Program scholarship, and her research presented at the XIX IBC was supported by the International Carnivorous Plant Society and the School of Biological Sciences at the University of Western Australia. AME was supported by grant 11-44056 from the US NSF.

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PROPAGATION OF SOME TUBEROUS *DROSERA* BY LEAF CUTTING

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Tuberous *Drosera* are a large and attractive group of sundews that have generally been of limited availability in cultivation because of their slow rates of propagation. They are usually available as dormant tubers or seed. However, seed can be difficult to germinate and seedlings slow to reach maturity. A few taxa reproduce asexually by the production of daughter tubers (e.g. *D. erythrorhiza* Lindl., *D. intricata* Planch., and *D. tubaestylis* N.G. Marchant & Lowrie) (Lowrie 2013)), but many remain as single plants for years. Most taxa are self-incompatible so flowering does not guarantee seed production. Tissue culture hastens seedlings to reach maturity, but not all taxa are in culture. Some novel means of asexual reproduction have been attempted, such as removing the tuber from plants in active growth (Pierson 1996), cutting dormant tubers in half (Pietropaolo & Pietropaolo 1986), or cutting sections of stem (Lowrie 2013: Vol. 1, pp. 38-40). Leaf cuttings have been used to propagate some erect-growing taxa (e.g. Pierson 1996; Powell 1989; Pietropaolo & Pietropaolo 1986) but this appears to have been overlooked in recent years. The technique I have used is described below.

Leaf cutting plants in nature

Vickery (1933) described plants of *Drosera auriculata* Backh. ex Planch. and *D. peltata* Thunb. in the wild with leaves that generated a stolon on the upper surface that may develop a tuber. The leaves were still attached to the plants and occurred in unusually humid conditions. She was able to generate such epiphyllous buds from plants and detached leaves in cultivation.

I have also observed leaf cuttings forming from leaves of *D. peltata* in wet locations the wild (e.g. Rowe & Gibson 1999), but it was not until the last few years when I took a new interest in this phenomenon.

Leaf cuttings in cultivation

In winter 2015, I cut some leaves of a cultivated *D. peltata* plant and planted them in a wet mix of equal parts peat moss and quartz sand in a pot of *Genlisea hispidula* Stapf that was growing inside about 15 cm from a fluorescent light. The petiole was placed in a small hole, which was then backfilled to snugly hold the detached leaf with the leaf blade at the surface of the mix. Over the next four weeks all but one leaf died. The surviving leaf remained green and formed a swollen bud on its surface from which a stolon formed that grew to the leaf edge and then grew into the mix. By early summer the leaf and stolon had died but a new tuber had formed. A new plant has emerged and grown each winter since then – but has yet to reach maturity.

In June 2016, I detached some leaves and the end of a leafy stem of a cultivated *D. gigantea* Lindl. plant. This time I placed these cuttings with their cut bases in a moist peat moss and quartz sand mix in a sealed rectangular plastic food container (Fig. 1). The container was placed by an east-facing window. Over the next few weeks most of the detached leaves formed a bud from which a stolon emerged that grew irregularly across the leaf surface. The swelling also produced a rosette of leaves less than 1 cm across. The detached stem fragment quickly rotted away save for the leaves which all produced stolons that grew into the mix. The new plants emerged in winter 1997 and formed small rosettes.

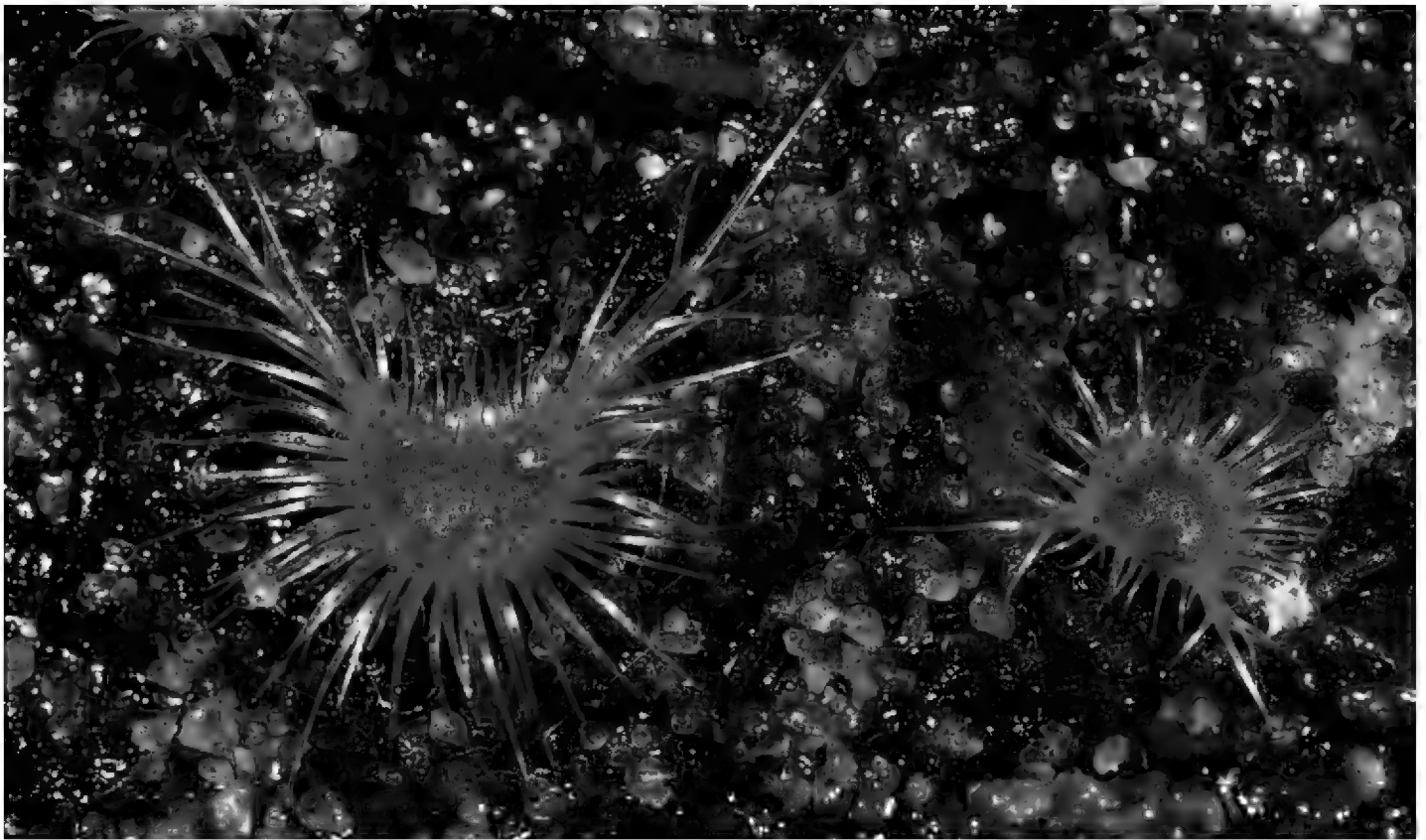


Figure 1: Six weeks after harvest these leaves of *Drosera gigantea* have epiphyllous buds that are developing a rosette of small leaves.

In July 2017, I detached three leaves from plants of *D. gigantea*, *D. macrantha* Endl., *D. stricticaulis* (Diels) O.H.Sarg., and *D. sulphurea* Lehm. The leaves of *D. macrantha* and *D. stricticaulis* rotted without producing any stolons; perhaps because these species are adapted to drier conditions? However, leaves from *D. gigantea*, once again, formed small buds within six weeks, from which stolons and small rosettes developed (Fig. 2). Sometimes the stolon did not clear the leaf blade and instead formed the tuber on the leaf surface, beside the rosette. Two of the *D. sulphurea* produced a stolon. One cleared the leaf blade, grew down about 1.5 cm long and formed a tuber about 2 mm diameter before the parent leaf died (Fig. 3). By early December 2017, the stolon on the other leaf had not reached the leaf margin but had a short leafy stem and developing stolon (Fig. 4).

The small sample has yielded a success rate of over 50% for *D. gigantea* and *D. sulphurea* leaf cuttings. Successful leaves form single tuber about 2 mm diameter within 4 or 5 months. The tuber may be left where it has formed (or buried the same depth as the tuber if it has formed on the parental leaf blade) where it will regrow the following autumn. They require a more humid version of the growing conditions of the parent plant to develop epiphyllous buds.

This technique offers a cheap and simple means of propagating some tuberous *Drosera* that otherwise tend to remain as single plants in a collection, and also in propagating attractive forms of some taxa – such as the all-red form of *D. gigantea*. While raising clones will not solve the problem of self-incompatibility it may provide a means of generating new stock to trade for different plants that may open the option of seed production in the future.

To date, it seems this technique works for erect-growing tuberous *Drosera* that are native to wet habitats. It appears likely to work for such taxa as *D. bulbigena* Morrison, *D. geniculata* (N.G.Marchant & Lowrie) Lowrie (e.g. see Lowrie 2013: Vol. 1, p. 39), *D. neesii* Lehm., and maybe even swamp-growing plants of *D. fimbriata* DeBuhr?

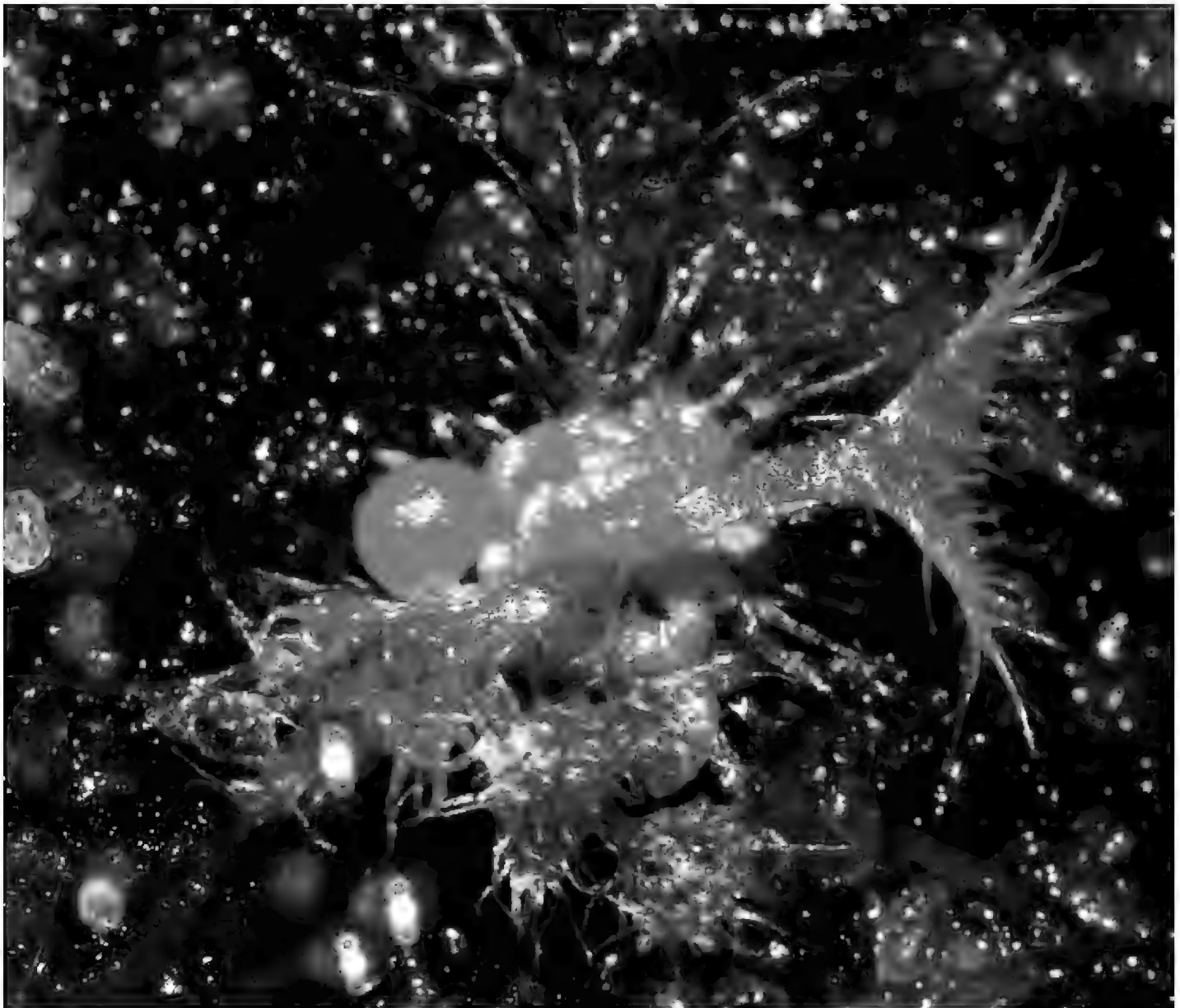


Figure 2: *Drosera gigantea* leaf cutting with a developing tuber. The parent leaf has rotted away.



Figure 3: *Drosera sulphurea* leaf cutting that formed a stolon and small tuber.

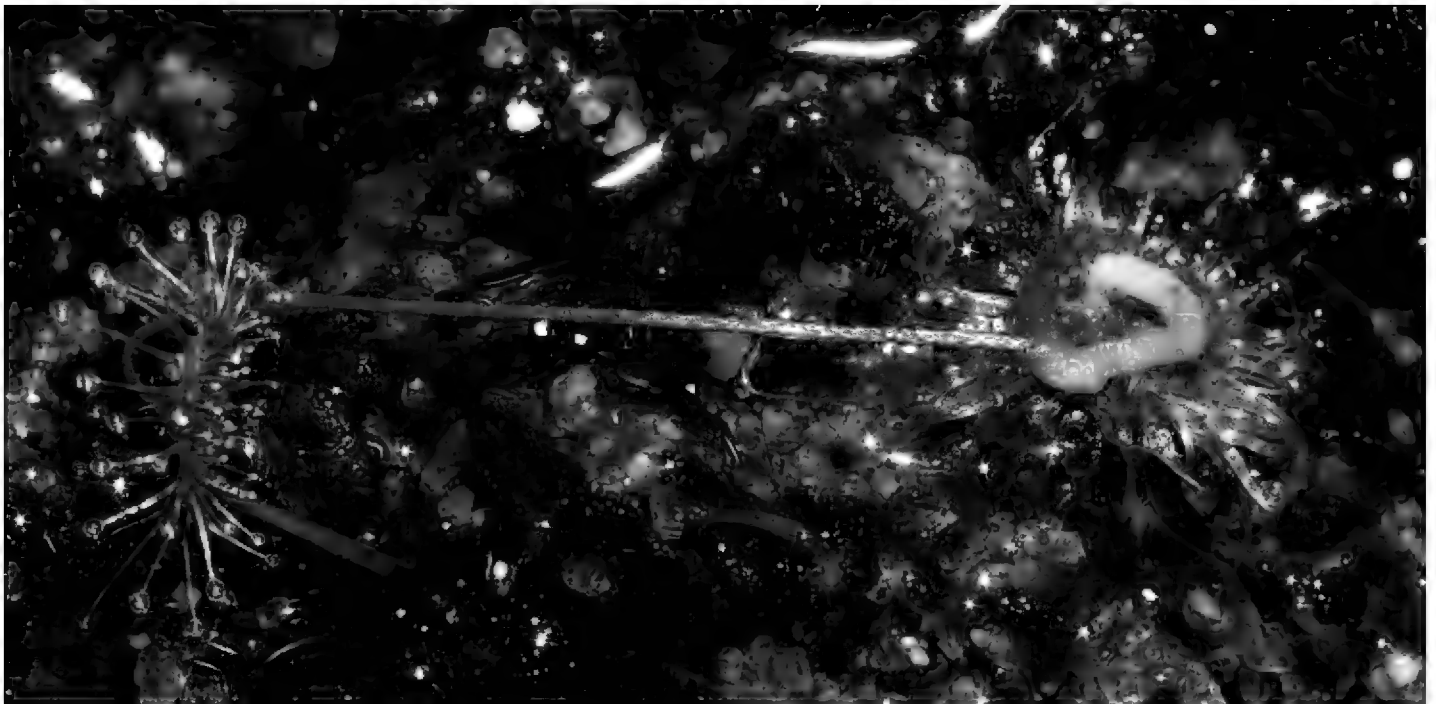


Figure 4: Epiphyllous bud of *Drosera sulphurea* with a leafy stem and a developing stolon.

Conclusions

Leaf cuttings are a viable way to propagate some taxa of tuberous *Drosera*. They have worked for a number of erect-growing taxa that tend to grow in wet conditions. This technique requires a small amount of plant material but offers a chance to propagate some very attractive plants. It is worth giving it a go.

Acknowledgements: I thank Greg Bourke, Kirk 'Füzzzy' Hirsch, Richard Jobson, and Ross Rowe for assistance with fieldwork in which observations of natural leaf cuttings of *D. auriculata* and *D. peltata* were observed in the wild.

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THE USE OF THE RIGHT WORDS:
WHY CARNITROPISM IS INACCURATE FOR CARNIVOROUS PLANTS.
SUGGESTION TO REJECT THE TERM “CARNITROPISM”

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Keywords: carnitropism, chemonasty, chemotropism, plant movement, thigmonasty, tropism.

Abstract: In the September 2017 issue of Carnivorous Plant Newsletter, the term ‘carnitropism’ was proposed to name triggered movements occurring in *Dionaea*, *Drosera*, and *Pinguicula* genera. However, those phenomena were misconceived and their interpretation lacked scientific background, misleading to a flawed conclusion. Therefore, the present paper recommends to avoid the use of that term and recalls both the mechanisms behind plant movements and their associated names.

Introduction

Simón (2017) explained that “*Plants are known to move towards certain stimuli (water, light, gravity) which are beneficial and these movements have been labeled hydrotropism, phototropism, geotropism.*” Yet, such a statement is very likely to bring confusion. For one thing, no definition of tropism including its physiological origin was clearly introduced in the article. A couple of examples cannot make up for that absence. For another, although tropism is indeed *an instance* of plant reaction to stimuli, that is not the sole one. Another kind of reaction, called “nastic movement” is actually more common when it comes to carnivorous plants. The main difference between these two mechanisms is found at the cell level, and could roughly be defined as such:

- Tropism is usually a growth movement due to uneven cell multiplication, which eventually leads to the organ orientation. A tropism is affected by a stimulus and its position. It can be positive (movement towards the stimulus) or negative (movement away from the stimulus).
- Nastic movement is usually a reversible movement due to hydraulic processes, e.g. change in cell turgescence. Such movement is always predefined by the motile structure and is thus independent of the direction of the stimulus (Boullard 1988; Gatin 1924; Jouy & de Foucault 2016).

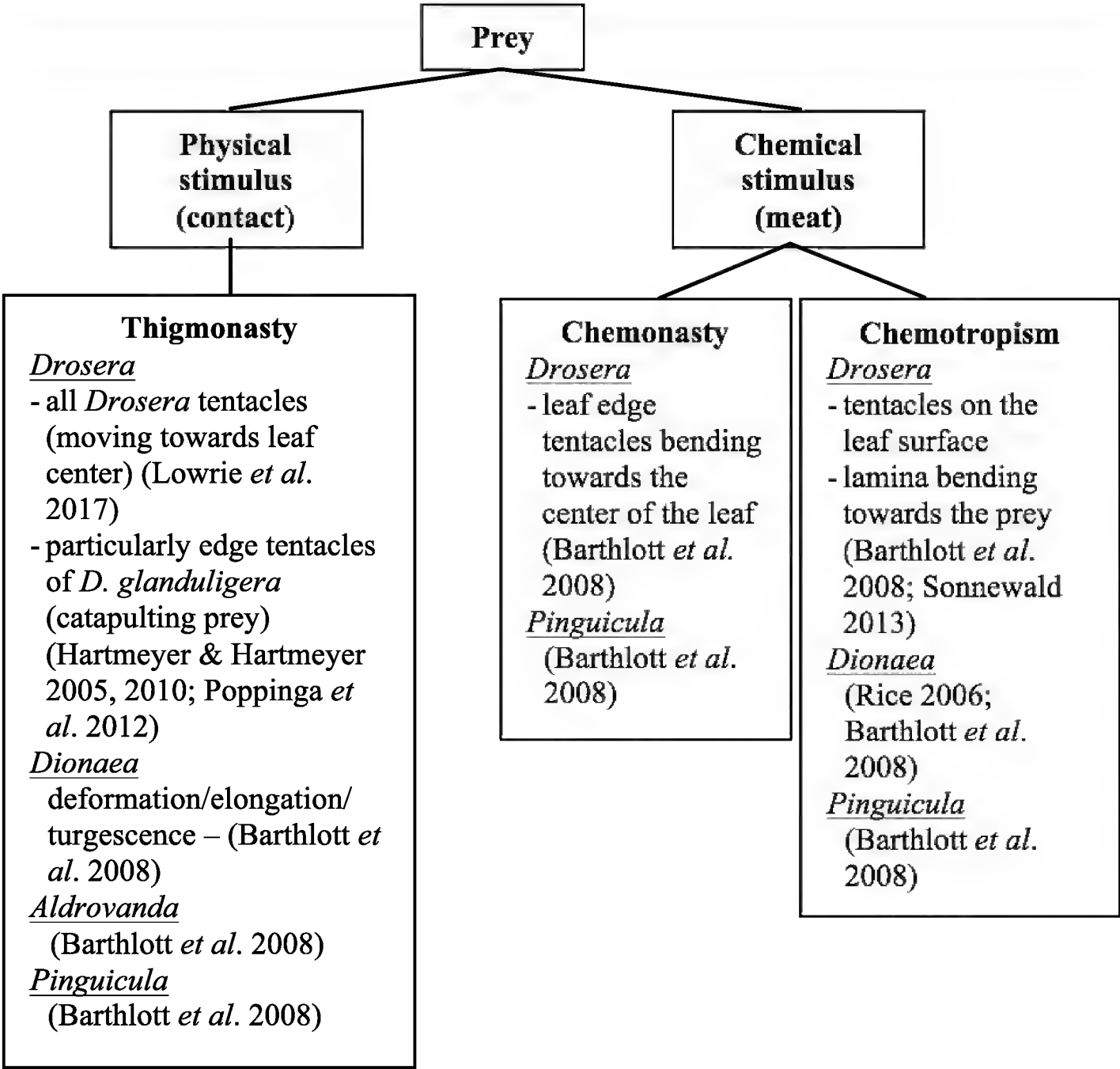
A same stimulus can induce those two kinds of movements. As quoted by Simón (2017), light stimulates phototropism. Plants kept on a windowsill will grow towards sunlight and this phenomenon is called positive phototropism. In addition, sunlight can also cause photonasty, i.e. nastic movement in response to a change in light intensity. For example, the alternation of opening and closing of flowers during day and night (e.g. *Mirabilis jalapa*, the four o’clock flower), or the bending of *Oxalis* leaflets at night.

When it comes to capture mechanisms associated with carnivorous plants, several movements are involved. Darwin (1875) himself established that the movement displayed by *Drosera rotundifolia* is due to two factors: contact and meat presence, or in other words, physical and chemical stimuli.

Contact stimulus induces thigmonasty

Some carnivorous plants exhibit active traps: prey are caught by quick movements, like *Dionaea* (Barthlott *et al.* 2008; Forterre *et al.* 2012), *Aldrovanda* (Cross 2012), and *Utricularia* (Tay-

Table 1. Summarized mechanisms in active and semi-active traps of carnivorous plants, with their associated stimuli (courtesy of V. Bazile).



lor 1989). It is also the case with some particular *Drosera* such as *D. glanduligera*, with external snap-tentacles catapulting visitors into the trap (Hartmeyer & Hartmeyer 2005, 2010; Poppinga *et al.* 2012). However, the origin of the trapping movement has often yet to be completely elucidated.

About the famous *Dionaea muscipula*, there is no consensus so far. Barthlott *et al.* (2008) suggested that it is a case of thigmonasty (nastic movement in response to contact) (Table 1). Specific cells, forming a sort of hinge, would undertake a vigorous turgor increase. This would result in their deformation and elongation, and ultimately in the trap closing. On the other hand, Legendre (2000) stated that a rapid multiplication of cells would be responsible for the snapping movement. Thus, the *Dionaea* trap does in no way perform a thigmotropism, although it is speculated that growth processes take place during trap lobe bending. The movement reaction (snapping) is always the same, independent to the direction of the triggering mechanical stimulus (S. Poppinga, pers. comm.).

As for *D. glanduligera*, Hartmeyer & Hartmeyer (2010) showed that upon stimulation, tentacles of *D. glanduligera* curve toward the lamina center and not toward the place where the stimulus occurred. Thus, this rapid catapult movement would clearly be a case of thigmonasty. In a less spec-

tacular fashion, thigmonasty is generally observed throughout the genus *Drosera*, with a first, slow movement of all types of stalked glands (Lowrie *et al.* 2017). Similar observations were made with *Pinguicula*: when stimulated by inorganic matter, the leaf margins slightly curve by thigmonasty, then recover quickly (Lloyd 1942).

Chemical stimulus induces chemonasty and chemotropism

Besides contact stimulus, *Drosera* leaves react to the presence of certain molecules (Darwin 1875), notably NH_4^+ ions (Sonnewald 2013). Such chemical excitation causes a slow movement of both adjacent tentacles and the whole lamina (Darwin 1875; Barthlott *et al.* 2008). Contrary to what Simón (2017) suggested, this phenomenon is a two-fold mechanism (Table 1).

The first mechanism is based upon a chemically-induced nastic movement (chemonasty). The “*edge tentacles of the leaf are dorsiventrally structured and react chemonastically*” as stated by Sonnewald (2013). These tentacles do react to meat compounds, but the mechanism itself is not determined by the position of those compounds. All the tentacles of the leaf lamina edge bend towards the center by rapid cell expansion regardless of the prey position (Lowrie *et al.* 2017).

The second mechanism does involve tropism but since it is a chemical stimulus, the accurate name is chemotropism and should consequently be used. As every carnivorous plant enthusiast might have observed, for example in *Drosera capensis*, a trapped prey is surrounded by both tentacles and the leaf lamina. In this case, the movement is driven by the position of the stimulus, as the leaf and tentacles bend precisely towards the prey. Furthermore, this movement is due to cell growth (Lowrie *et al.* 2017), induced by increased growth hormone production (Barthlott *et al.* 2008) and can thus be considered as a tropism. According to Lloyd (1942), this mechanism was first observed by Batalin (1877) and later more explored by Hooker (1916, 1917). Tentacles bend towards the prey, stimulated by NH_4^+ ions among others (Sonnewald 2013).

Likewise, the sole presence of dead prey on a *Pinguicula* leaf induces movements. First, a chemonastic reaction takes place as the lamina surface becomes slightly concave due to a change of turgescence. It eventually forms like a small tray filled with leaf exudates (Barthlott *et al.* 2008; Rice 2006). Then, a chemotropic reaction follows as leaf margins bend towards the nutrient source, leading to the wrapping of the prey. Although this movement is very easily confused with the thigmonastic reaction triggered by contact stimulus, like Darwin did (1875), Lloyd (1942) showed that this wrapping movement is actually attributable to growth.

Finally, in *Dionaea muscipula*, after the trap closing due to thigmonasty, presence of organic compounds (such as ammonium, sodium, uric acid, coprostanol) entails a more complete closing by chemotropism (Barthlott *et al.* 2008). Both lamina lobes slowly approach each other, then shut the trap hermetically (Bailey & McPherson 2012). Here again, cell growth causes the movement (Rice 2006).

Conclusion

1. Leaf and tentacle movements in *Drosera*, *Pinguicula*, and *Dionaea* are due to several mechanisms.
2. The discussed mechanisms have had a name for a long time: thigmonasty, chemonasty, and chemotropism.

Acknowledgments: The author would like to thank Dr. Bob Ziemer for his suggestion to write a rebuttal, Dr. Aymeric Roccia and Dr. Vincent Bazile for their reviews and their support and Dr. Jan

Schlauer for having kindly pointed out some relevant information, supplying essential bibliography, and offering to review this rebuttal. The author would also give a special thanks to Dr. Simon Poppinga, from the University of Freiburg, who concomitantly wrote a valuable paper about the same subject, and kindly decide to withdraw his paper in favor of the present article.

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NEW CULTIVARS

Keywords: cultivar, *Sarracenia* 'Lilianna', *Sarracenia* 'Leviathan', *Drosera* 'Hercules'.

Sarracenia 'Lilianna'

Submitted: 27 October 2017

Sarracenia 'Lilianna' is the sister plant of *Sarracenia* 'Leviathan', coming from the same crossing of *S. leucophylla* × *S. flava* var. *maxima*., as grown by Chris Rawlings.

The tallest pitcher height recorded so far is 99 cm, with the average largest pitchers on all examples being well over 85 cm.

There are numerous differences that mark *Sarracenia* 'Lilianna' as distinct compared to *S.* 'Leviathan'. *Sarracenia* 'Lilianna' has a narrow but striking throat blotch, which gathers again at the very edges of the throat (Fig. 1).

Overall a dark crimson veination is present. The veining is bold and more pronounced, particularly on the lid, where it bleeds all the way to the edges of the rim. The lid's coloring is cream rather than white and the green of the pitcher extends further up the back of the lid.

The pitchers feature strong, yet intermittent white areolation, which extends further down the tube than on *S.* 'Leviathan'.

The plant is named for Mrs Lilianna Rawlings, Chris's wife, who has supported his obsession growing out his massive *S. moorei* for over 20 years.

This plant should only be reproduced by vegetative means to ensure that its unique characteristics are maintained. Those interested in obtaining divisions should contact us using the email address below.

—PAUL YOUNG • Bristol • England • GBR

—STEVE SULLIVAN • Penarth • Wales • GBR • s.sullivan5@btinternet.com

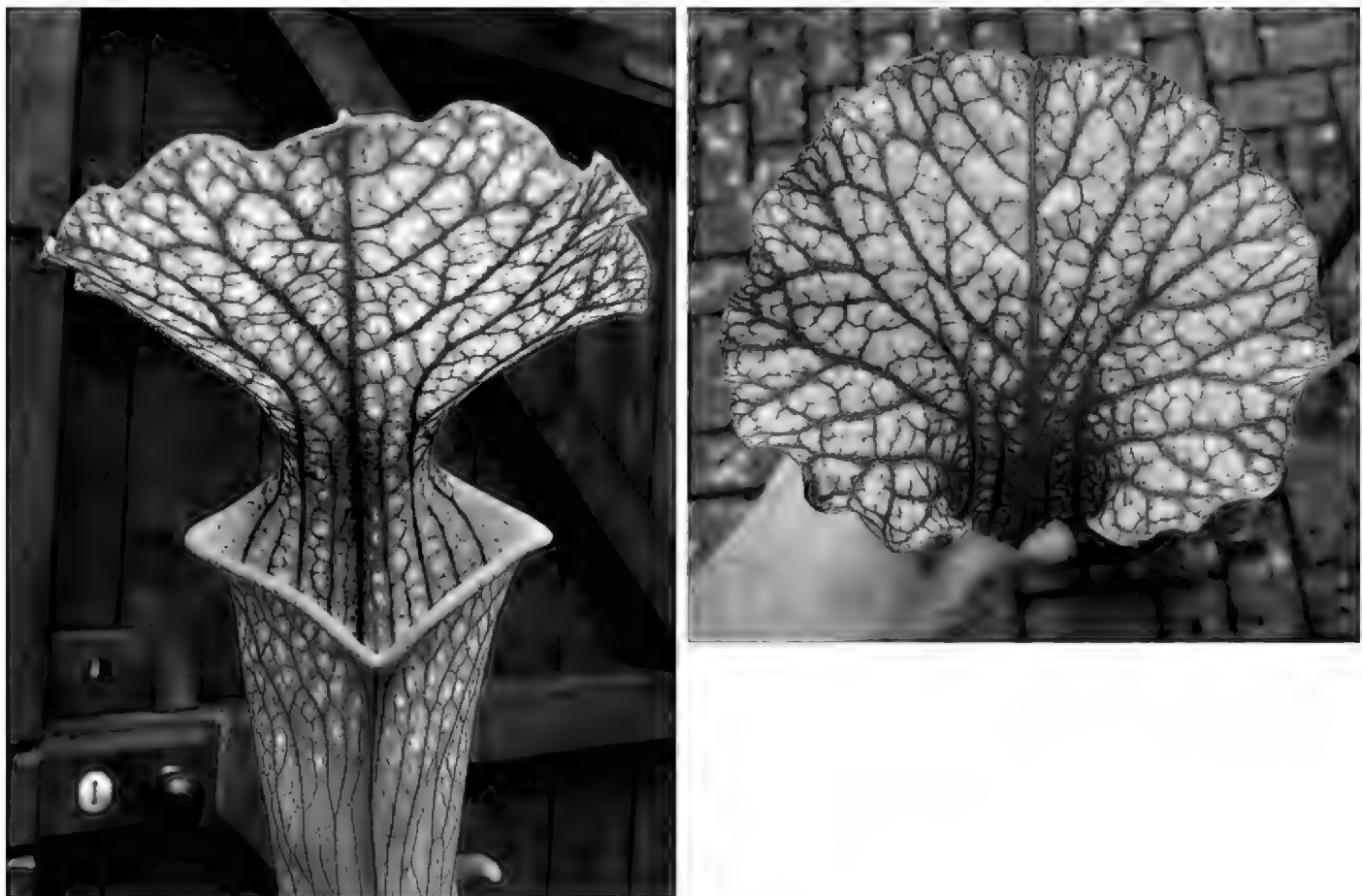


Figure 1: *Sarracenia* 'Lilianna'. pitcher (left) and lid (right).

Submitted: 27 October 2017

Sarracenia 'Leviathan' is truly a monster *S. moorei*. The average tallest pitcher height of this *Sarracenia* across the divisions we witnessed is over 100 cm, with the largest spring pitcher seen so far growing to a gigantic 123 cm! (Back Cover).

Sarracenia 'Leviathan' was recently discovered growing in the private collection of Chris Rawlings of Bath, England. Chris's collection contains mainly plants he personally acquired from Adrian Slack during the 1980s.

Sarracenia 'Leviathan' was seed grown by Chris from his own hybrid of *S. leucophylla* × *S. flava* var. *maxima*. It is one of only two seedlings he grew out from this cross (see *Sarracenia* 'Lilianna' for the other), both of which he selected for their amazing size and vigor.

The pitchers are lime green, with light red veining and white fenestration appearing near the very top of the pitcher (Fig. 2). The mouth features striking red venation and a strong red throat blotch. The lid itself is white with paler red venation. Flower coloration appears to be inherited from *S. flava* var. *maxima*, being sulphur yellow in appearance.

The plant is named after a towering biblical monster from the depths, in this case from the depths of Bath!

This plant should only be reproduced by vegetative means to ensure that its unique characteristics are maintained. We will be dividing the plants we have acquired and making them available to fellow collectors during dormancy. Please contact us using the email address below to reserve a division.

—PAUL YOUNG • Bristol • England • GBR

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Figure 2: *Sarracenia* 'Leviathan' pitcher, including flies! (left) and lid (right).

Submitted: 18 December 2017

Drosera ‘Hercules’ is a clone of the hybrid *D. capensis* ‘Albino’ × *D. aliciae*. I did not breed this plant and its origins are unknown to me. I acquired it from Matt Byers of California in Fall 2016. Matt has lost his record of his original acquisition.

The plantlet I received from Matt quickly grew into a monster. The growth habit of this sundew primarily resembles *D. capensis*. It produces a slowly ascending stem, long petioles, and strap-shaped leaves (Fig. 3). Its flower scapes are long and hirsute, are not glandular, and the flowers are pink. Stipules are present, but are less prominent than in *D. capensis*, and remain triangular. The tentacles are red, and the whole plant follows the color patterns of a typical *D. capensis* when grown under artificial lights.

The qualities of *D. aliciae*, however, endow this spectacular sundew with strikingly broadened features, including its laminae, which are only slightly wider than its petioles. The leaves last a long time before atrophying, and barely reflex. The result is a broad-leaved plant bearing many erect leaves on stocky petioles.

Auxiliary roots on *D.* ‘Hercules’ are produced frequently. The plant has a tendency to clump as well, and its many fleshy roots tend to outgrow their containers.

Drosera ‘Hercules’ is a fast-growing specimen with excellent qualities valuable to the horticulturalist. It is resilient and recovers quickly from pruning, fast to reproduce from cuttings, and most of all, impressive. The term Phil Faulisi used to describe *D.* ‘Hercules’ was “stud”. Hybrid vigor in *D.* ‘Hercules’ is very apparent, in its toughness and the ability in larger plants to produce many leaves at a time. The silent drama of the oar-shaped leaves of ‘Hercules’ ensconcing a maimed cricket is nothing short of satisfying. Displaying large specimens of ‘Hercules’ at Oregon gatherings has drawn the curiosity of many.

This plant was originally distributed by me under the names “Juggernaut” and “Corinthian”, alluding to both its bold impression and its architectural elegance. As “Juggernaut” was never my first choice to name the plant, and as *Drosera* × *corinthiaca* is a different hybrid which already includes *D. aliciae*, I decided to name this impressive sundew ‘Hercules’. In ancient Greek mythology, Hercules (Heracles) is the demigod son of Zeus and the mortal lady Alcmene. From birth a figure endowed with great strength and charisma, the god-cult of Hercules spread throughout the ancient world. I can only hope that *Drosera* ‘Hercules’ flourishes just as well.

This plant should be propagated vegetatively to preserve its unique characteristics.

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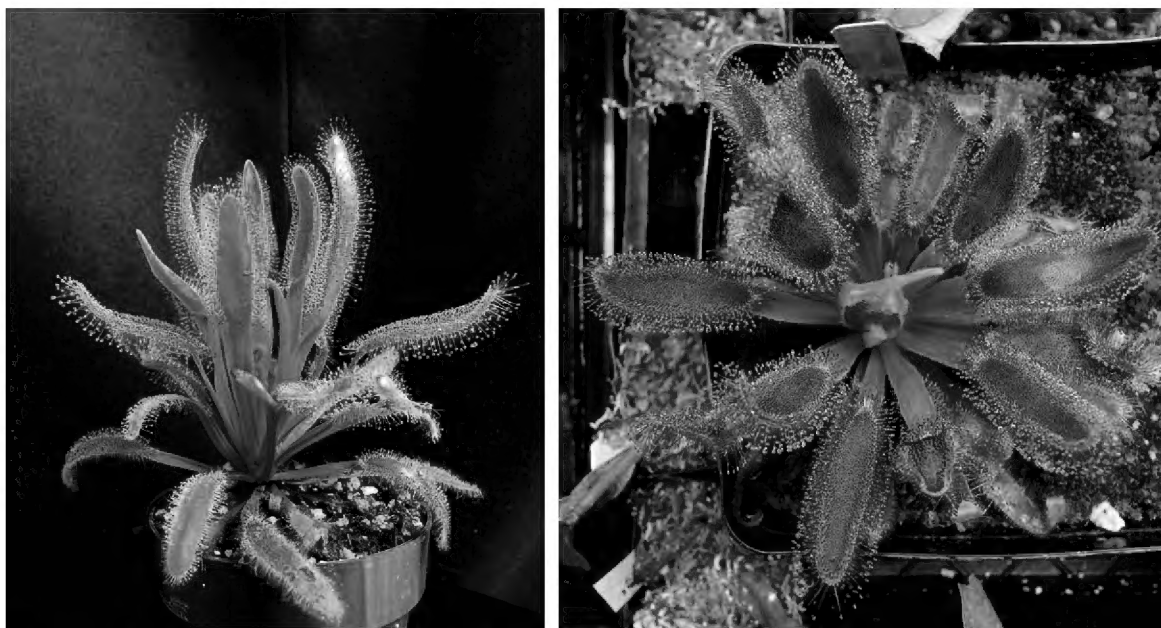


Figure 3: *Drosera* ‘Hercules’ side and top view.

REGISTER NOW FOR THE ICPS FIELD TRIP (7-11 AUGUST 2018)

The best times of my life have been spent in the company of dear friends looking at and photographing carnivorous plants in the wild. There's something so special and magical about seeing these rare and ancient plants in the very spot that they evolved millions of years ago. It shall be our great pleasure to share these native carnivorous plants with experts and enthusiasts alike from all over the world. We invite you to register quickly as it is first come first serve.

We've gathered a tight crew of experts to lead the fieldtrip: Daniela Ribbecke, Gina Morimoto, Arthur Yin, Barry Rice, Harry Tryon, and myself. Daniela and I run California Carnivores. Arthur and Gina are longtime enthusiasts with lots of experience in the field. Barry is a well-known expert and author and Harry knows more about *Darlingtonia* than anybody else. Honestly, we're also a bunch of characters too. The company and comradery are half the reason to go on these trips. We laughed until our cheeks hurt on the planning trip, so we know it's going to be a blast!

The Cobra Plant, *Darlingtonia californica*, has a strange alluring beauty. Their translucent heads and long red mustaches glow in the evening sun and make for stunning photos. Late Summer is one of the best times to see the cobra plants! We've planned the trip to show a diverse range of *Darlingtonia*, *Drosera*, and *Pinguicula* habitat. We'll see roadside cliffs where carnivores cling to the wet rocks and we'll travel down dirt roads into California back country to see stands and stands of *Darlingtonia*. The trip will culminate with the famous Days Gulch at Eight Dollar Mountain where the *Darlingtonia* march in a wide swath over 100 meters up the mountain. It's considered by most to be the very best *Darlingtonia* site.

Cobra plant country is itself spectacular. You'll be able to examine and photograph *Darlingtonia*, *Drosera rotundifolia*, controversial *Drosera capensis*, and *Pinguicula macroceras* all against the gorgeous, wild back-country of the Pacific Northwest. We expect to see Roosevelt elk (*Cervus elaphus roosevelti*) on the drive up and we'll drive through and walk amongst ancient redwoods. The rivers are pristine, crystal clear, and emerald green. It was the home to the Gold Rush and remains to this day the Wild West. Words can't hope to do this area justice—so again we're excited to invite you on this once in a lifetime trip!

—DAMON COLLINGSWORTH

Registration: <http://www.icpscon2018.com>



